Action prediction and the development thereof

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Table of Contents

About the Cover

Bicycles are a means of transportation in the Netherlands and people do not stop using their bike when they become a parent. Consequently, there are many sorts of bike seats available that enable parents to take their infant or toddler with them on their bike. Around the age of 4, children learn to ride a bicycle. Of course, they start out with short distances, and hence will for some time still be transported on their parent's bike for the more purposeful trips.

There was a day, when my oldest daughter had just learned how to ride her bicycle, on which I had to bring her younger brother and sister to daycare. On our way back, my daughter, sitting on the bike seat right behind me commented when I had to ride up a small (small small) hill: "Now you need to pedal harder. Here we are going uphill." Several days later, I went to the supermarket, again, the oldest sitting in her bike seat. She said: "This is hard, because of the wind." For almost four years, she had regularly been transported by us as parents, on our bikes. Never had she mentioned the circumstances that affected the biking difficulty. But now that she was able to ride a bicycle herself, she showed that she was aware of the action context. Only anecdotal evidence of course, but experience might matter.

Chapter 1

General Introduction

Being able to understand and predict what other people are doing has major benefits in everyday life. If I understand that your action of filling ground coffee into the coffee maker will lead to a pot of coffee that we can share, then I can save my energy and do not need to get up to make coffee myself. If you can predict my walking action, you can adjust your pace and direction to avoid unwanted collisions. If a child nagging for lemonade sees her mother picking up the lemonade bottle, the child can (in principle…) stop nagging once she recognizes that mother has started the action sequence that will lead to the desired end product.
The question for the cognitive researcher is *how* we get to understand and predict others' actions. Which mechanisms underlie action prediction and action understanding? The question for developmental research is *when* these capacities come into place, and more intriguing even, *what mechanism* drives the development of action understanding and action prediction? These questions form the heart of the current thesis, which focuses on action prediction and the development thereof.

Action understanding and action prediction

What does it mean to understand an action? A detailed theoretical analysis by Uithol and colleagues (Uithol, van Rooij, Bekkering, & Haselager, 2011) showed that action researchers use multiple definitions of action understanding interchangeably. What is meant by the term action understanding can go from rudimentary forms as action classification ("This is grasping a cup"), to action anticipation ("Preparing a hand action to grasp the offered cup") to more complex matters such as recognition of the action purpose ("The cup is grasped to drink"). The latter assumes that observers can read the intention of the actor from the action itself. Although it would be very beneficial for the development of social cognition if infants were capable of doing this, it is a matter of debate whether they actually can. Some scholars claim that infants can indeed grasp the intention underlying an action from an early age on through reasoning (Gergeley & Csibra, 2003). According to such accounts, 14-month-old infants are believed to be capable of relatively complicated reasoning. For instance, infants might judge it more sensible for a model to use her head to turn on a light when her hands are occupied compared to when her hands are free, because then she might as well have used her hands to turn on the light (Gergely, Bekkering, & Király, 2002). In an empirical test of this hypothesis, a higher proportion of infants imitated turning on a light with the head (rather than using their hands) when they had previously observed a model switching the light on with her head who had her hands free compared to a model acting similarly, but with occupied hands. Recent studies have provided low-level explanations to explain this finding (Paulus, Hunnius, Vissers, & Bekkering, 2011d, 2011e). One should thus be cautious to avoid the over-interpretation of infant data (Haith, 1998; Schöner, & Thelen, 2006; Heyes, 2014), and it seems safer to not draw strong conclusions about the potential intention reading abilities of infants who cannot verbally report on their interpretation of other's intentions (Hunnius & Bekkering, 2014).

Action prediction, on the other hand, is more directly measurable. With action prediction, I mean that the observer has an expectation about the future state(s) of an observed action. For instance, an observer might predict the end location of an action or make a prediction about which object in the scene will be grasped by an actor. Predictions can be measured explicitly, by asking observers where an action will end before it has actually ended, but predictions can also be measured more implicitly by analyzing where observers look while the action is still unfolding (Flanagan & Johansson, 2003). If an infant observes an actor grasping a cup and looks to the cup before the hand arrives there, this indicates that the infant predicted what would happen. Hence, gazing at locations where the actor will move next is an indication of action prediction. Visually tracking an action also indicates action prediction. The sensory system is relatively slow and, therefore, tracking a moving target requires predictions, otherwise the eyes would constantly lag behind (Rosander & von Hofsten, 2002). In contrast to most other definitions of action understanding, the necessary step from the concept of action prediction to its operationalization is small. An observer has predicted an action if she has expectations about when and where the action will end before the action is completed. Measuring the quality of this prediction can be done by investigating where the observer looked during the action and when. The ability to predict actions is based on skills and knowledge acquired throughout the life-span, but is likely to develop fast in the first years of life. Investigating social cognitive development, by studying action prediction in infancy is therefore the core aim of the current thesis.

What types of information can potentially be used to predict others' actions?

It is clear from previous research that infants and adults are capable of predicting others' actions (Hunnius & Bekkering, 2010; Falck-Ytter, Gredebäck & von Hofsten, 2006; Ambrosini et al., 2013). However, it is less clear what types of observable information present in the action are used for action prediction. Actions are thought to contain several elements: 1) an agent, 2) a target or goal, 3) movements of the agent, 4) a context or environment. Next, the role of these action aspects for action prediction will be reviewed, followed by a discussion of the development and mechanisms that allow these aspects to become a basis for action prediction.

The agent

Naturally, an action is carried out by an agent. An agent is an entity that can act on its own (Leslie, 1995). The identity of the agent can affect action prediction in multiple ways. First of all, agency ascription may play a role in action prediction. In other words, agents must display certain properties - agency cues - to be identified as agents. For instance, objects normally cannot move out of themselves, self-propelledness is therefore a clear agency cue (Premack, 1990). According to the naïve theory of rational action, only the movements of objects or people to whom the observer ascribes agency, can be predicted (Gergely, & Csibra, 2003). The issue of agency and its effect on action prediction is briefly touched upon in the experiments reported in Chapter 5 of this thesis. There, the objects are either self-propelled (Exp. 1), or their movement are externally triggered (Exp. 2). Second, having prior knowledge about the agent affects the interpretation of an action and predictions resulting from the interpretation. For example, a hand moving a scalpel is more likely to be perceived as "to cure" if the hand belongs to someone identified by the observer as a doctor, compared to when the hand seems to belong to a criminal (Kilner, Friston, & Friston, 2007; Jacob & Jeannerod, 2005).

The action target

Many studies in action perception research emphasize the role of action goals or targets (Grafton & Hamilton, 2007). The term "goal" can refer to a specific location (a cup can for instance be brought to the mouth), to a specific object (for instance a ball which is being grasped; see also Uithol et al., 2011), or even to mental states

(Gallese, Rochat, Cossu, & Sinigaglia, 2009; Iacoboni et al., 2005). In the current thesis, the term “target” is adopted, which refers to the object an action is directed at (examples can be found in Chapters 3, 4, and 6) or, more broadly, the location where the action will end (examples can be found in Chapters 2 and 5). Many authors have expressed the idea that targets are more important than means, as there might be an infinite amount of means to achieve the same outcome (Wolpert, 1997; Kilner et al., 2007). Identifying the potential target of an observed action allows the observer to narrow down her predictions concerning the potential movements, but in theory only to a limited extent because of the possibly unlimited ways to achieve the same outcome. To test whether the presence of a potential target indeed leads to more accurate predictions, a series of experiments was conducted, which can be found in Chapter 3. There, the presence of a target was manipulated to investigate how this affects predictions of the movements of the actor. Many infant prediction studies only include one potential target. In Chapters 4 and 6 we therefore investigated whether observers are capable of predicting the actual target of an action when multiple but distinct targets are present.

The movements

To what extent movements are useful as a basis for action prediction is debatable. As many different movements can be used to reach the same target, movements seem not very helpful at first. The view that targets are more important than movements for action perception has been prominent in the last few decades (Woodward, 1998; Jovanovic et al., 2007; Bekkering et al., 2000; Umiltà et al., 2008). Behaviorally, children were shown to prioritize goals over means by imitating the goal rather than the means of an action (Bekkering, Wohlschläger, & Gattis, 2000), and action targets were shown to bring about more interference in responding to action-related questions than means (van Elk, van Schie, & Bekkering, 2008). Mirror neuron research with macaque monkeys seemed to indicate that the action target and not primarily the means to achieve the target is encoded by mirror neurons, as these neurons were shown to fire for object-directed actions only (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Furthermore, monkeys were trained to grasp objects with normal and reversed pliers. The movements necessary for handling the reversed pliers are the opposite of those needed with the regular pliers in order to achieve the same goal. The mirror neurons of these trained monkeys responded in the same phase of the action, indicating that mirror neurons encode goals, not movements (Umiltà et al., 2008).

This research stands in contrast with recent empirical work that illustrates that movements *do* have a clear impact on action perception. For instance, observers can judge based on the kinematics of lifting movements whether an actor held false beliefs about the weight of the lifted object (Grèzes, Frith, & Passingham, 2004a). When intending to cooperate with an interaction partner, the kinematics of a grasping action are different compared to when intending to compete (Becchio, Sartori, Bulgheroni, & Castiello, 2008), and observers are indeed capable of dissociating these actions from each other (Sartori, Becchio, & Castiello, 2011). Due to this clear tension between different views on the role of movements, the current thesis addresses the role of movements for action prediction in many of the chapters. In Chapter 2, the relative impact of movements on action prediction is contrasted to the impact targets may have on action prediction. In Chapters 5 and 6, the quality of action prediction based on movements is investigated.

The action context

Another element of an action is the environment or context in which the action takes place. The action context may shape action predictions (Kilner et al., 2007). This is illustrated by an fMRI (functional Magnetic Resonance Imaging) study by Iacoboni and colleagues (2005) that tested whether the action context changes activation of the mirror neuron system (activation of premotor areas) in observing adults. The participants viewed a table with objects that were related to drinking a cup of tea. The objects where either positioned such that they were representative of a situation before drinking tea compared to just after drinking tea. Though the context itself did not evoke a different response in the targeted brain areas, in combination with a hand grasping a cup, different brain responses were found. The observers' premotor mirror neuron areas responded more strongly to the grasping action if the context indicated "before having tea", compared to "after having tea", which according to the authors meant that observers responded more strongly to grasping with the intention to drink than to grasping with the intention to clean up the table. In the current thesis, the role of visible context of the action in action prediction is investigated in Chapters 3 and 4. The visible context in this case concerns action constraints which shape actions, such that the same movements without these constraints can be considered inefficient. That is, a detour is justified when an obstacle lies in-between the actor and her target, but this detour is unnecessary in the absence of such an obstacle. In this way, action constraints can render the exact same movements into an efficient means to achieve a target or an inefficient means.

Action efficiency is also a prominent aspect of one of the experience-independent accounts on action prediction development, which is the topic of the next section. From the review below, it will become clear that taking a developmental approach when investigating action prediction also sheds light on the processes underlying action prediction in general.

Experience-independent accounts

An important distinction between theories on action understanding is whether the developmental processes for acquiring action understanding are thought to be experience-dependent or experience-independent. A prominent theory of the latter class is the naïve theory of rational action (Gergely & Csibra, 2003). In this theory, infants are thought to make use of abstract rules to infer unseen aspects of an action, and are assumed to expect agents to act rationally, namely choosing the most efficient route to achieve their goal. For instance, agents should take the shortest possible path, taking into account obstacles in the environment. In one of the paradigms often used to empirically test the theory of rational action (Csibra, Bíró, Koós, & Gergely, 2003; Csibra, Gergely, Bíró, Koos, & Brockbank, 1999; Gergely, Nádasdy, Csibra, & Bíró, 1995), a ball rolls over the floor and then jumps over a vertical obstacle to get to another ball (the target). Infants are repeatedly presented with this jumping event until they lose interest and have become habituated. After habituation, infants are presented with two different test trials, which both no longer contain the vertical obstacle. In the one test trial, the agent takes the same path with a jump, which is now an unnecessary detour. In the other test trial, the agent moves in an efficient, straight line trajectory towards the other ball. The typical outcome is that infants look longer at the test trial containing the detour, which is interpreted as the child being surprised about the agent taking an inefficient path (see Csibra et al., 1999, 2003; Gergely et al., 1995). The infants' surprise also shows that, according the authors, infants *expect* agents to use an efficient means to achieve their goal, and the unexpected inefficiency leads to a surprise reaction.

On the hand, the naïve theory of rational action is elegant as infants only need to consider two elements (for instance, the path and the obstacle) to infer the third element of an action (the goal), and the elements can be left out interchangeably: the infant can infer the goal from the path and the obstacle as easily as she can infer the path from the goal and the obstacle. On the other hand, it leaves the developmental researcher somewhat puzzled, as the theory is implicit about how development is expected to unfold. How can infants expect others to move efficiently from A to B if they never locomoted from one location to another themselves? (Amy Skerry and colleagues for instance propose that action experience is a prerequisite for sensitivity to action efficiency, see Skerry, Carey, & Spelke, 2013). And what forms of efficiency are taken into account by the observing infants? At present, rationality theory provides no explicit definition of efficiency. Both the head touch paradigm and the jumping-ball paradigm can be viewed as examples of minimization of path length, but also as examples of minimization of consumed energy and minimization of time. And what does this theory tell us about action prediction? The rationality principle is not only used to explain infants' emerging action understanding, it is also supposed to form the basis for action prediction. But then, can we draw conclusions about action prediction based on looking times in a habituation paradigm? Sensitivity for a violation of efficiency which is measured in the habituation experiments, in which infants first repeatedly watch an efficient event, might not automatically lead to the ability to predict the outcome of an action based on the efficiency of the action while the action is still unfolding. Recently, Szilvia Bíró (2013) carried out an eye-tracking study using the jumping-ball paradigm in which she investigated whether infants predict the end location of the jumping ball in the presence or absence of an obstacle. Infants displayed predictive eye movements for both the efficient and the inefficient action condition. In the first experiment, predictions were made quicker in the efficient compared to the inefficient condition, though this result was not replicated in the second experiment. In a similar vein, other eye-tracking studies displaying long and short paths have revealed that even adults do not predict an actor to take the short path the very first time they see the actor choosing this efficient path (Kayhan, Monroy, Hunnius, Gerson, & Bekkering, in prep.; Paulus, Hunnius, van Wijngaarden, Vrins, van Rooij, & Bekkering, 2011). Thus, although efficiency can in theory be a very useful principle to base action predictions on, it is still unclear whether it is used in everyday life, as the empirical results summarized here indicate that efficiency principles are not necessarily applied in the first instance, not even by adults.

More accounts are available arguing that action prediction and action understanding can develop independently from experience (Luo, & Baillargeon, 2005; Baron-Cohen, 1997; Johnson, 2000; Leslie, 1995; Premack, 1990), but it goes beyond the scope of this thesis to describe these accounts in depth. A common factor shared in experience-independent views is that no improvement in action prediction abilities should be found with – for instance – growing motor abilities or increasing visual experience. Another hypothesis stemming from the experience-independent viewpoints is that prediction accuracy should be action-unspecific and only depend on individual prediction capabilities.

Experience-dependent accounts

In contrast, experience-dependent viewpoints share the idea that experience is necessary for action prediction and that experience improves action prediction. Generally, two types of experiences can be distinguished, namely perceptual and motor experience. As most studies on action prediction focus on visual paradigms, only the role of visual experience will be discussed, although the same principles likely also hold for other sensory modalities (see e.g., Aliu, Houde, & Nagarajan, 2008 on expectations of auditory action-effects, and Blakemore, Wolpert, & Frith, 2000 on expectations of somatosensory action-effects).

Visual experience

If there is one thing in the world that we like to look at, it is other people. By merely observing other people's actions, infants can form associations between different aspects of actions that normally follow each other (Buchsbaum, Griffiths, Gopnik, & Baldwin, 2009; Monroy, Gerson, & Hunnius, submitted). For instance, they may learn that a hand reaching for a cup often is followed by the cup being brought to the mouth (Hunnius & Bekkering, 2010). Studies on visual perception have shown that associative learning is a powerful learning mechanism in infancy (Fiser & Aslin, 2002; Slater, Mattock, Brown, Burnham, & Young, 1991; Younger & Cohen, 1986). Not only are infants able to form associations between perceived events (Saffran, Johnson, Aslin, & Newport, 1999), they can also use these associations to predict future events. Haith and colleagues (Haith, Hazan, & Goodman, 1988) demonstrated that 3.5-month-old infants learn to fixate at the location where an event will take place when the event sequence follows a regular pattern, whereas infants of 6 to 9 weeks of age do not yet show this predictive behavior consistently (Robinson, McCarty, & Haith, 1988).

Visual experience with sequences hence can later form the basis for predicting future states of these observed sequences, and this can apply to actions as well. A recently conducted eye-tracking study in our lab tested whether infants can predict observed action sequences based on statistical learning (Monroy et al., submitted). Infants observed a continuous stream of actions consisting of 6 unique actions that were repeated in the sequence. The stream consisted of several action pairs which followed each other with a transitional probability of 1, meaning that that action was always followed by a specific next action. Other actions were presented in random order with transitional probabilities ranging between 0.25 and 0.33. Infants displayed more frequent anticipatory looks to the upcoming action of an action pair than to any of the other potential actions. Half of the infants were not presented with a hand performing the actions, but the actions took place without any human involvement. Infants in this “event” condition did not look more frequently ahead to the upcoming second action of pair. This implies that infants can use statistical regularities in action sequences to predict the upcoming action, but only if the action is performed by a human.

Purely observational experience with actions can lead not only to the formation of associations between two visual events, it can also lead to the formation of visuo-motor associations. But how can an observer build associations between her own motor code necessary to carry out these actions and the visual consequences of another person’s action, *without* having performed this action herself? This can be achieved if we adopt the viewpoint that an action constitutes movements of the actor and action effects which manifest themselves in the sensory domain. In the action execution domain, the thought is that the motor code for an action and the percept stemming from the action effect become associated when frequently experiencing both the action and its effect (Elsner & Hommel, 2001; 2004). When the association is formed, the action effect can activate the motor code while the previous actor is now inactive, only perceiving the action-effect. In the action observation domain, a novel action effect might become bound to a motor code in the observer using a similar principle: the observer views an actor making a movement which results in an action effect. The observer’s motor system gets activated because the movements are in her motor repertoire. Over trials, an association between the motor code and the percept of the action effect may be established in the observer, this time without having performed this particular action herself. Hence, if a person is capable of performing an action, then observing that action with a novel action-effect may lead to associations between the motor code and the action-effect (Elsner & Aschersleben, 2003; Paulus, van Dam, Hunnius, Lindemann, & Bekkering, 2011; Paulus, Hunnius, & Bekkering, 2013). In this way, even if the observed actions are never performed by the observer, she might still have acquired sensorimotor associations of these actions, which may be used for action prediction.

Motor experience

As already briefly touched upon in the previous section, motor experience might play a role in action prediction. To explain how action prediction can be facilitated by motor experience, I will first review findings on motor system involvement in action perception, followed by a discussion of the role of motor experience in action perception development. Based on these developmental accounts, I will explain how motor experience might influence action prediction.

Motor system involvement in Action Perception

During the last decade, many studies have examined the role of the motor system in action perception. Already in 1954, Gastaut and Bert showed that action perception can influence the electroencephalographic (EEG) signal in a similar way as action execution does. Likewise, theories proposing a link between action and perception (see e.g. Prinz, 1987; Greenwald, 1970; Gibson, 1979; James, 1890; von Hofsten & Lee, 1982) were formulated well before the discovery of the so-called mirror neurons in macaque monkeys in the early 90's of the past century that provided support for the link between action and perception on single cell level (Rizzolatti et al., 1996a; Gallese et al., 1996). Mirror neurons received their name because they were shown to respond to performed as well as to observed actions. A debate followed on whether or not humans also possess mirror neurons (Lingnau, Gesierich, & Caramazza, 2009; Turella, Pierno, Tubaldi, & Castiello, 2009; Hickok, 2009; Kilner, Neal, Weiskopf, Friston, & Frith, 2009; Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). Now, there is relatively broad consensus that humans have a mirror system (MS; Rizzolatti, 2005; Aziz-Zadeh, Koski, Zaidel, Mazziotta, & Iacoboni, 2006; Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007; Catmur, Walsh, & Heyes, 2007), sometimes also called an action observation network (AON; Cross, Kraemer, Hamilton, Kelley, & Grafton,2009; Neal & Kilner, 2010), which responds in a comparable way to observed actions as it does during the execution of actions. Evidence for this comes from studies using different neuroimaging methods, such as fMRI (Binkofski et al., 1999; Buccino et al., 2001; Iacoboni et al., 1999; Koski et al., 2002; Grèzes, Armony, Rowe, & Passingham, 2003), Positron Emission Tomography (PET; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Rizzolatti et al., 1996b; Grèzes, Costes, & Decety, 1998), Transcranial Magnetic Stimulation (TMS; Heiser, Iacoboni, Maeda, Marcus, & Mazziotta, 2003; Fadiga, Craighero, & Olivier, 2005; Fadiga, Fogassi, Pavesi,& Rizzolatti, 1995; Cattaneo, Sandini, & Schwarzbach, 2010; Catmur, Walsh, & Heyes, 2007), and electrophysiological methods including magnetoencephalography, (MEG; Hari et al., 1998; Nishitani & Hari, 2000; 2002; Kilner, Marchant, & Frith, 2009). This vast amount of evidence brings up the question what purpose the action observation network might serve, if any. If the action observation network serves to facilitate action understanding, its development is an important topic to study when one wants to unravel the mechanisms behind action understanding. That is, studying the development of the action observation network not only provides information about the developmental timeline of the network, it might also shed more light on how the functions of the network come into place.

Only a handful of methods can be used to measure neural motor activation in infants. TMS, MRI, and PET are considered invasive and hence not preferable for testing children. Though MEG is not invasive, it is rarely used with children as a special and expensive helmet is required to allow the measurement of all brain areas simultaneously. Hence, researchers assessing motor activation are left with EEG or functional Near Infra-Red Spectroscopy (fNIRS) as relatively direct measures of motor activation and with imitation as a more indirect measure. The motor resonance account of imitation postulates that if the motor system of an infant is activated while observing the model's actions, the chance is higher that the infant will imitate the action (Paulus et al., 2011d). Imitation scores can therefore be a measure of motor activation, though only in an indirect way, as the relation between motor activation during observing the model's actions and the subsequent imitation does not need to be one-to-one. More directly, neural motor activation can be measured using EEG and fNIRS. The EEG signal contains oscillations of different frequencies, and several frequency bands have been associated with motor functioning. Specifically the mu-frequency band (around 8-12 Hz in adults, Pfurtscheller, Neuper, & Krausz, 2000; Kuhlman, 1978) and the beta-frequency band (18-35 Hz in adults, Stancák Jr,, & Pfurtscheller, 1996; Jasper & Penfield, 1949; Conway et al., 1995) display reduced power when the owner of the brain is moving. A similar suppression of the mu- and beta-frequency bands has been found during action observation (Pineda, 2005; Muthukumaraswamy & Johnson, 2004; Muthukumaraswamy, Johnson & McNair, 2004; Cochin, Barthelemy, Lejeune, Roux, & Martineau, 1998; Kilner et al., 2009; Hari et al., 1998). Developmental studies have shown that infants' mu-frequency power (for more information about the development of this frequency band, see Marshall, Bar-Haim, & Fox, 2002) decreases during action execution (Stroganova, Orekhova, & Posikera, 1999; Southgate, Johnson, Karoui, & Csibra, 2010; Marshall, Young, & Meltzoff, 2011) as well as during action observation (Southgate et al., 2010; Marshall et al., 2011; Nyström, Ljunghammar, Rosander, & von Hofsten, 2011; van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008).

The development of the Action-Perception link

There is an ongoing debate in the field about how this link between action and perception comes into place. Some scholars claim that it is present at birth (see e.g. Lepage & Théoret, 2007; Craighero, Leo, Umiltà, & Simion, 2011). Others postulate that the link comes into place with age through maturation, independently from experience (see e.g., Csibra, 2007; Southgate, 2013). As a third alternative, the perception-action link may be acquired through sensorimotor experience (see e.g., Heyes, 2010; Hunnius & Bekkering, 2014). A fourth approach, which entails a strong claim, would be that motor experience alone is enough for the formation of the perception-action link (see e.g., Casile & Giese, 2006).

The empirical test for a nativist viewpoint is to investigate newborns. Frequently cited evidence for an inborn action-perception link is the work of Andrew Meltzoff on neonatal imitation (Meltzoff & Moore, 1977; 1983). The argument here is that if a newborn is capable of replicating the facial movements they observe in others, she must possess a mechanism that matches the observed actions onto the newborn's own body and movements. Meltzoff and Moore (1997) explicitly leave room for a combination of experience-dependent and experience-independent viewpoints, as they mention that infants might have gained sensorimotor experience in the womb, for instance by experiencing the feelings caused by moving their mouth. However, other nativists seem to leave no role for active experience in acquiring the perception-link. For example, neonates are expected to have sensorimotor links for actions they are incapable of performing themselves (Craighero et al., 2011). Although the studies on neonatal imitation are frequently cited, scholars have had trouble replicating the famous findings on neonatal imitation (see for an overview Anisfeld, 1991; 1996; Ray & Heyes, 2011). It seems especially problematic that infants reliably imitate only tongue protrusions, as this behavior can also be a result of heightened arousal levels during the imitation phase (Jones, 2006).

Alternatively, the action-perception link may come into place through maturation (Csibra, 2007; Southgate, 2013). In Csibra's view, an observer first makes a goal inference when observing an action outside the motor system. Based on this goal inference, the action that is necessary to bring about the goal is emulated in the motor system. Thus, an infant can link perception to action as long as the observed action can be emulated in the motor system. But when can an action and when can an action *not* be emulated? The theory does not provide an explicit answer to this question, but presumably, the infant must have some motor capabilities, be they sparse. If an actor is observed grasping an object with the foot and the observers is capable of achieving the same goal, namely grasping the object, but with a different effector, the observer is still capable of emulating the action. But in the absence of motor abilities to achieve the same goal, emulation should not be possible. A related view can be found in Victoria Southgate's work, who theorizes that infants can use their motor system to understand and predict actions of other agents. Infants do not need to be able to perform the observed action, but supposedly rely on a general motor plan to run simulations to predict observed actions. In this way, infants can also use their motor system for understanding biologically impossible actions (Southgate & Begus, 2013). Development in this account comes from general motor maturation.

A contrasting third view is that the action-perception link comes into place through accumulation of sensorimotor experiences. The most explicit mechanistic description of how sensorimotor experience might instantiate the perception-action link is elegantly described by Cecilia Heyes (2010; a more elaborate description can be found in Cook, Bird, Catmur, Press, & Heyes, 2014). The link between action and perception is thought to come into place through associative learning based on the accumulation of sensorimotor experience. That is, when a person moves, both the motor code necessary to perform the action and the percept resulting from the motor code are active. If the sensory code and the motor code are contingent and contiguous, an association between the motor and sensory code is established. Based on the acquired association, observation of the action performed by someone else can then activate the associated motor code. For actions that cannot be observed by the person performing them, such as frowning, the association is supposedly formed upon viewing someone else imitating you (Catmur et al., 2007).

The suggestion that sensorimotor experience is a prerequisite for the link between action and perception leads to a number of testable hypotheses. Amongst others, the association between a motor code and the corresponding perceptual code of an action must be exclusive: performing action A leads to sensory consequences A, and as a result an association will be formed between motor code A and percept A, whereas based on this experience, no association will be formed between motor code A and a non-related percept B, nor will there be an association formed between motor code B and percept A. If this theory holds, then experts in specific sports should show differential motor responses to observing their own sport compared to novices. This approach was taken by Calvo-Merino and colleagues (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard 2005), who showed that the motor system of ballet dancers is more strongly involved when processing others' ballet compared to capoeira dance moves, whereas the opposite holds for capoeira dancers. A logical question flowing from these results is what the role here is of visual experience, as ballet dancers not only have more experience performing ballet dance moves, they also perceive ballet dance moves more frequently. In a follow-up study, ballet dancers observed in the fMRI scanner dance moves of their own gender, which are highly motorically familiar, and dance moves of the opposite gender, which are highly visually familiar. The results confirmed that motor rather than visual experience strengthens the action-perception link, as ballet dancers of both genders responded stronger for own compared to opposite gender ballet dance moves (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006). Of course, these were dance moves acquired prior to the study, in contrast to the study of Emily Cross and colleagues (Cross, Hamilton, & Grafton, 2006), who tested ballet dancers 5 times in an fMRI experiment during a 5-week period in which they learnt a new type of dance. The dancers displayed stronger motor activity when observing the newly learned dance movements compared to control dance moves, and the effect increased with training duration. A comparable question has been addressed in a study with 14- to 16-month-old infants (van Elk et al., 2008b). Infants of this age have a considerable amount of crawling experience, but hardly any to no walking experience. Mu-frequency power was significantly lower when observing crawling than when observing walking movements. Thus, experience with crawling seems to affect the motor involvement when observing crawling. Indeed, individuals with longer crawling experience also showed a stronger effect in the action observation setting. Differences in crawling experience were due to the natural variability in crawling onset. In line with these findings, a recently published study testing 10-month-old infants has demonstrated that motor training but not visual training induces motor activation when infants later perceive the sensory consequences of the trained action (Gerson, Hunnius, & Bekkering, 2014).

The role of Motor Experience for Action Prediction

The overwhelmingly large body of research showing that the motor system is activated during action observation begs the question what the functional role of the motor system is in action perception. A widely accepted idea is that the motor system is involved in action perception to allow an observer to predict future states of others' actions (Kilner et al., 2007; Prinz, 2006; Wolpert, Doya, & Kawato, 2003). Where did the idea originate that the motor system might be used for action prediction? Studies on action production show that people predict the sensory outcomes of their own actions (Wolpert & Flanagan, 2001; Wolpert, Miall, & Kawato, 1998; Jordan & Rumelhart, 1992; Wolpert, Ghahramani, & Jordan, 1995). As sensory information arrives only after a relatively long delay at the central nervous system, feedback of the sensory system comes in relatively late during the action and relying on such feedback is hence not very effective. Therefore, when initiating movements, the motor system generates predictions about the expected sensory outcomes of the initiated movement. These predictions stem from forward models (Wolpert et al., 2003; Wolpert & Flanagan, 2001) which are supposedly acquired through action experience. Moreover, sensory outcomes become associated with motor commands through sensorimotor learning. Once the associations are formed, they can be used in the forward model to predict upcoming sensory states. Empirical evidence for this mechanism stems from research with robots (Demiris & Dearden, 2005) and adults (Sailer, Flanagan & Johansson, 2005). An eye-tracking study of Flanagan and Johansson (2003) showed that adults' gaze behavior for observing a block-stacking task was highly similar to gaze behavior when performing a block-stacking task. Gaze was already focused on the next target location before the hand arrived there with the next block, and gaze was thus predictive both in action execution as well as in action observation. It is fascinating that gaze was not predictive when the hand was not visible in the observation condition. Apparently, simulation and prediction of the action can only take place if the actor can be observed. Inspired by these results, Falck-Ytter and colleagues (2006) tested whether infants of 6 and 12 months of age would display similar predictive gaze patterns when observing an actor placing an object in a container. While 12-month-olds are capable of reaching and grasping, and putting objects in buckets, 6-month-olds are not. Based on their motor abilities, the authors expected only the 12-month-olds to predict the placing action, in contrast to the 6-month-olds. The results of the study revealed the 12- but not the 6-month-old infant indeed looked at the container before the hand arrived. Potentially, prediction of an observed action relies on motor experience with this action. Follow-up studies have shown similar results: infants more readily make an inference about the end location of an action if the action is within their motor repertoire (Kanakogi & Itakura 2011; Cannon &Woodward, 2012; Gredebäck & Kochukhova, 2010).

Summary

It becomes clear from the literature described above that there are multiple mechanisms on which predictions of observed actions can be based. In principle, purely visual experience might be enough to predict the future states of ongoing actions. However, a growing body of literature suggests that motor experience might play a crucial role in action prediction. Furthermore, abstract rules and knowledge about objects may inform action prediction as well. The current thesis aims to shed more light on what types of information from the observed actions are used to predict future states of the action (Chapters 2, 3, 4, 5, and 6). Furthermore, the mechanisms potentially underlying action prediction (Chapters 2, 4, 5, and 6) and the development of action prediction (Chapters 4, 5, and 6) are examined.

To that end, Chapter 2 describes a study in which infants observed actors lifting a cup to the mouth or a phone to the ear, which are ordinary actions. The infants also observed unusual actions, in which the actor brought a cup to the ear or a phone to the mouth. Infants are capable of predicting where actions with these objects normally end (Hunnius & Bekkering, 2010), presumably through visual experience with these actions. Chapter 2 thus provides an example of action prediction based on previously acquired object-knowledge.

Chapter 3 focuses on the contribution of several types of information for action prediction, namely the role of contextual information, the presence or absence of a distinct target object, and the kinematics of the actor. To further elucidate the role of contextual information in the *development* of action prediction, Chapter 4 reports a study on two groups of infants and a group of adults who observed an efficient and an inefficient action. In this study, the kinematics of the actor were held constant, as was the presence and location of the target object. The efficiency of the action was defined through the manipulation of the context, which afforded walking or necessitated a relatively inefficient mode of locomotion (i.e. crawling). In both situations, the actor crawled, and the question was whether the inefficiency of the crawling where it was unnecessary would be better detected by infants capable of walking compared to infants who had crawling but no walking experience. Chapter 5 depicts two experiments in which the role of motor experience for action prediction was investigated. If prediction of a specific action requires motor experience with exactly that same action, then an action like walking should be more accurately predicted by those capable of walking compared to those yet incapable. Similarly, we expected in Chapter 5 that infants who are able to aim at and press small buttons, would be more accurate in predicting aiming actions. Three groups of infants and a group of adults observed a hand aiming for and pressing a large or a small button. The movement is quicker for a large than for a small button, and the specific question in Chapter 6 was therefore whether the velocity of the action could be used for predicting whether a button would be the target or not. If motor processes underlie these speed-based predictions, then predictions should be more accurate for observers capable of performing the action compared to those yet incapable. The chapters describing the experimental results (Chapters 2 to 6) are followed by a summary of the main findings and a discussion of the implications of the findings in Chapter 7.

Chapter 2

Motor Activation During Observation of Unusual Versus Ordinary Actions in Infancy

Abstract

Infants make predictions about actions they observe already during the first year of life. To investigate the role of the motor system in predicting the end state of observed actions, 12-month-old infants were shown movies of ordinary and extraordinary object-directed actions. The stimuli displayed a female actor who picked up an everyday object (a cup or a phone) and brought it to either her mouth or her ear. In this way, a similar movement could be ordinary (e.g., cup to mouth) or extraordinary (e.g., phone to mouth) depending on the object used. Infants' EEG and eye movements were recorded. We found a significantly stronger motor activation, indicated by a stronger desynchronization in the mu-frequency band over fronto-central areas, during observation of extraordinary compared to ordinary actions. This is explained within the computational framework of Kilner and colleagues (2007), who suggest that the motor system is used to generate predictions about actions we observe. If the observed action deviates from the initially expected path, additional predictions have to be generated, resulting in a stronger motor activation during perception of extraordinary actions. In sum, it appears that from early in life, the motor system is involved in making predictions about how an observed action will end.

Keywords: Infant; EEG; Action prediction; Motor system

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Introduction

From the first days of their life, infants watch their environment and the people acting in it. Recent research has demonstrated that infants form expectations and make predictions about others' actions. Looking time studies, for instance, show that infants tend to look longer at actions that end in an unexpected way (Phillips, Wellman, & Spelke, 2002; Reid, Csibra, Belsky, & Johnson, 2007; Woodward, 1998). Neuroimaging studies also suggest that infants respond differently to unexpected action endings (e.g., Reid et al., 2007, 2009). Moreover, infants as young as 6 months show predictive eye movements to the target area of actions they observe (Falck-Ytter et al., 2006; Hunnius & Bekkering, 2010). However, which functional mechanisms underlie infants' action predictions is still an open and intriguing question.

Infants take account of situational and contextual cues in their predictions of action goals. For instance, infants appear to have expectations about where an action should end based on the functional objects that are involved in the action. In a recent study of Hunnius and Bekkering (2010), infants between 6 and 16 months of age were presented with stimulus movies in which a person brought three everyday objects (a cup, a phone, and a hair brush) to either the normal target area associated with that object (a cup to the mouth, a phone to the ear, etc.) or to an extraordinary target area (e.g., a cup to the ear). Infants displayed more frequent predictive looks to the action target when the objects were brought to the ordinary target area. Thus, already early in life infants form expectations about the course of an action on the basis of their knowledge about the involved objects.

How do infants come to predict the goal of an action on the basis of the different cues they perceive? Previous research has shown that both in adults (e.g., Borroni, Montagna, Cerri, & Baldissera, 2005; Cochin, Barthelemy, Roux, & Martineau, 1999; Hari et al., 1998) as well as in infants (Southgate, Johnson, Osborne, & Csibra, 2009) the motor system becomes active not only during the execution but also during the perception of actions (a phenomenon called *motor resonance*). Moreover, a large body of literature suggests that the motor system may be crucial in the prediction of action goals during both action observation and execution (see, e.g., Csibra, 2007; Kilner et al., 2007; Prinz, 2006; Wolpert & Flanagan, 2001). For actions to be executed smoothly, we need to make predictions and cannot rely solely on feedback from the sensory system as this would simply be too slow. Therefore, the motor system is thought to function through forward and inverse models (Wolpert et al., 1998). These models, which predict the course of an action, need to integrate information about the environment, such as objects that are acted upon. The same models that enable action execution to run smoothly can be used to generate predictions about actions we observe. Previous electroencephalography (EEG) studies indicate that the motor system is involved in a predictive manner during action observation, as motor-related EEG components appear to be modulated ahead of time (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004; Southgate et al., 2009). Kilner and colleagues (2007) proposed a computational model of how the mirror neuron system (MNS) can generate predictions of which goal is driving an observed action. The model, which functions as a Bayesian network, strives to minimize the error between the predicted action path and the observed action path. The predictions about what an action should look like given an assumed goal are thought to be generated by the motor system. During action observation, the MNS continuously checks whether the goal ascribed to the action still matches what is being observed. In the case where an unusual or unexpected action is observed, there is an initial mismatch between the observed and the predicted action, and subsequently new predictions need to be generated. This is thought to result in stronger motor activation. In sum, the model implies stronger motor activation during observation of actions that are hard to understand, or that unfold differently than assumed beforehand.

Motor activation can be measured with several neuroimaging methods. One of the most frequently used neuroimaging methods for studying the infant brain is EEG because of its noninvasiveness and because it imposes only minimal restrictions on the normal behavior of the infant. In the EEG, motor activation becomes apparent as a desynchronization in the mu-frequency band. Oscillations in the mu-frequency band are thought to originate from sensorimotor cortex and are found maximal over central and precentral sites (Pineda, 2005). Desynchronization in the mu-frequency band overlying central sites has been demonstrated during action observation both in adults (e.g., Gastaut & Bert, 1954; Muthukumaraswamy et al., 2004) and in infants (Southgate et al., 2009; van Elk et al., 2008b) and appears to be stronger for object-directed actions than for actions without objects (Muthukumaraswamy et al., 2004; Southgate et al., 2010). Moreover, mu-desynchronization has been shown to be stronger if the observed action is well established in the infant's motor repertoire (van Elk et al., 2008b).

It was the aim of this study to investigate whether the motor system is differentially activated during infants' perception of ordinary and extraordinary actions.

Twelve-month-old infants were repeatedly presented with stimulus movies displaying ordinary or extraordinary actions (e.g., an actor bringing a cup or a phone either to her mouth or to her ear). Infants' EEG was measured and concurrently, their eye movements were registered to investigate overt action predictions. By measuring motor activation in response to action observation, as reflected in desynchronization in the mu-frequency band of the EEG, we aimed to test the following hypothesis. If motor system activation reflects the discrepancy between the initial prediction of the action on the basis of previous knowledge and the actual observed action, we hypothesize that stronger motor activation would occur for observation of extraordinary compared to ordinary actions. That is, based on previously acquired object knowledge infants have expectations about the course and target of the observed actions (Hunnius & Bekkering, 2010). In a case where the observed action does not match the infant's expectations, new predictions have to be generated, thereby resulting in a stronger motor activation.

METHOD

Participants

In total, 36 12-month-old infants participated in the study. Measuring EEG and eye movements in 12-month-olds in parallel turned out to be difficult. Twelve infants contributed sufficient artifact-free EEG trials to be included in the EEG analyses. The mean age of this group was 12 months and 5 days (*SD* = 10 days), and the group comprised 8 girls. For 11 infants, sufficient eye movement data were collected during the experiment (i.e., gaze information present for more than 50% of the testing time). This concerned 7 girls, and the mean age of this group was 12 months and 5 days (*SD* = 11 days). Seven infants contributed both eye movement data and EEG data.

Procedure

Infants were tested in an action observation setting. During stimulus presentation, their EEG and their eye movements were recorded with a Tobii eye-tracking system (Tobii 1750, Tobii Technology, Danderyd, Sweden). The child was seated in a regular car seat at approximately 60 cm distance from the computer screen. Before testing, the eye-tracker was calibrated using the Clearview software (Tobii Technology). A nine-point calibration procedure was used in which at every position of a screen-wide 3 x 3 grid expanding– contracting circles appeared on a black background. To draw the infants' attention to the calibration stimuli, the circles were presented together with a sound. If seven or more points were calibrated successfully, the experiment was started. Otherwise the calibration procedure was repeated for the missing calibration points in the grid.

Two movement tilt sensors (CW60A/30; Comus Group of Companies, Tongeren, Belgium) were attached to the infant's arm and leg to record limb movements during the experiment. Trials during which the infant moved were excluded from the EEG analysis, as body movements would confound the data. The experiment was conducted using a custom-made stimulus presentation and data registration program implemented in Presentation 12.1 (Neurobehavioral Systems, Albany, CA, USA). In addition, the test sessions were video-recorded and coded offline to exclude trials during which the infant did not attend the screen (offline coding was necessary when eye gaze was not captured by the eye-tracker), and when the child was moving (offline coding was necessary when infants had removed the movement sensors).

Stimulus material

Infants watched movies of approximately 6 s in which a female actor who was sitting at a table grasped an object with her right hand and brought it either to her mouth or to her ear. The objects were a cup and a phone. These are both common everyday objects with distinct target areas (mouth, ear). In the Ordinary action condition, the phone was brought to the ear and the cup to the mouth (see Figure 1a for an example), whereas in the Extraordinary action condition the phone was brought to the mouth and the cup to the ear (see Figure 1b). The actor's looking behavior was kept constant between the conditions, and she never looked straight into the camera. All stimulus movies had a similar time course: First, the actor was looking at the object in front of her without any movement for about 1 s; then the actor grasped the object, lifted it and brought it either to her mouth or ear. When the object reached its target area, the actor held the object in this end state for approximately 1 s. The movement path of the grasping and lifting was similar in all conditions, and only after the object reached approximately the height of the actor's head did the paths diverge, depending on the end location. For each of the four conditions, six different movies were created with small variations to keep the infant interested (6 different phones and 6 different cups). Each movie was presented 5 times, and the stimuli were presented in blocks of 10 movies of the same condition. An advantage of presenting ordinary and extraordinary actions in different blocks is that it enhances semantic processing in contrast to random presentation, which is thought to evoke processing via a more automatic visuo-motor route (Tessari, Canessa, Ukmar, & Rumiati, 2007; Tessari & Rumiati, 2004). Within blocks, the order of the trials was randomized. All stimulus material was recorded with two female actors. The infants always watched one actor displaying the ordinary actions and the other one displaying the extraordinary actions. This contingency in the stimulus presentation was intended to give the infants' predictive system a maximal chance to work, as predictions of action end states are always based on a combination of the action itself and contextual information (van Rooij, Haselager, & Bekkering, 2008). Which actor displayed the correct actions was counterbalanced between participants.

The visual angle of the movies was 21.7° in the vertical direction and 21.5° in the horizontal direction. The angles of the movements were approximately 14° (vertical) and 12° (horizontal).

A

B

Figure 1: Example stimuli used in the experiment. (A) Snapshots taken from a stimulus used in the Ordinary × Mouth condition. (B) Snapshots taken from a stimulus used in the Extraordinary × Ear condition.

Eye-tracking

To register eye movements, an infrared eye-tracking system which was integrated in a 17-inch computer screen was used. The eye-tracker recorded the infants' gaze data continuously with a sampling rate of 50 Hz.

Analysis of the eye movement data

The amount of eye movement data per infant was considered to be sufficient for analysis if gaze data were available for at least half of the testing time. As the eye-tracking system is sensitive to head movements, for some babies eye data was gathered during only a part of the experiment. On average, 15 to 18 trials could be included per condition and participant. A visual anticipation was defined as a fixation in the target area of the action before the object reached this area. The coordinates of the mouth and ear target areas (areas of interest, AoIs) were defined for each individual stimulus movie. The size and dimensions of these rectangular target areas were identical for each condition (see Figure 2). For each stimulus movie, the lifting phase was identified during which the object was lifted from the table towards the target area. The end of the lifting phase was defined as the last frame before the object entered the mouth area. For each trial, it was determined whether the infant was attending to the actor and the action during the lifting

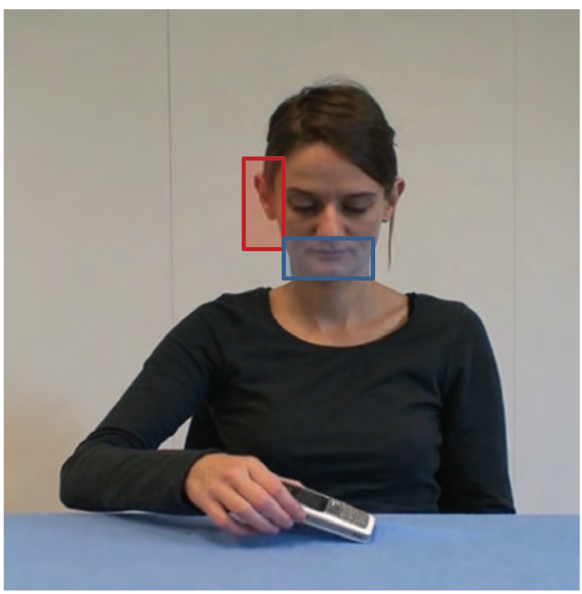

Figure 2: Areas of interest for the eye movement analysis. The blue rectangle depicts the mouth area used for the analysis of the anticipatory looks; the red rectangle depicts the ear area.

phase. Then, whether the proportion of the trials during which the infant showed an anticipatory fixation was different for Ordinary vs. Extraordinary stimulus movies was determined. A custom-made software tool (GSA, Donders Institute, Nijmegen, The Netherlands) was used to process the eye movement data and define whether and when fixations were in the AoIs. To test for differences in *frequency of anticipatory looks* between Ordinary and Extraordinary actions, a 2 x 2 repeated-measures analysis of variance (ANOVA) was conducted, with Target area as a second independent factor. Due to the limited overall number of visual anticipations, *latencies of anticipatory looks* could only be analyzed with the data collapsed over the two Target area conditions. The latency of the eye movements was defined as the difference between arrival of the eye gaze at the AoI and the object reaching the area of interest. A paired-samples *t*-test was used to test for differences in the latencies of anticipatory looks between the Ordinary and the Extraordinary action conditions.

Electrophysiological recording

EEG was recorded using a BrainCap with 30 Ag/AgCl electrodes (EasyCap, Herrsching, Germany) with a layout following the 10/20 system. All electrodes were referenced online to the left mastoid and re-referenced offline to the linked mastoids. A Brain-Amp AC amplifier using a bandpass filter of 0.1–80 Hz was used to record the EEG signal at a sampling rate of 500 Hz. The data were analyzed with Brain Vision Analyzer (Brain Products, Gilching, Germany).

Analysis of the EEG data

Artifact rejection was done manually on EEG segments that started with the lifting of the object and ended after 1200 ms. This interval was based on the average duration of the lifting phase and corresponded to the time window of the eye-movement analyses[1].

Infants were included in the EEG analyses if their EEG dataset contained at least 9 trials per condition that met the following criteria: (1) attention to the stimulus (based on eye-movement data, or, if missing, on the video recording of the test session), (2) no limb movements, (3) no EEG artifacts (such as eye blinks,

1 In the eye movements analyses, the exact time frame could be used from the start of the lifting movement to the last frame before the object entered the AoI. This resulted in small differences in window of analysis for each stimulus. For the EEG analyses, fixed time-windows were used instead, because frequency analysis requires fixed-length intervals.

electrode drifts, or broadband noise). Over each trial, fast Fourier transformations (FFTs) were conducted with the maximal spectral resolution (.833 Hz) over the 1200 ms interval. For each infant, the peak in the power of the mu-frequency band was identified by averaging the power over conditions and over the central electrodes (FC1, FC2, FC5, FC6, C3, Cz, C4, CP1, CP2, CP5, CP6) and plotting the log of the power against the frequency axis (see Figure 3a). Infants showed clear peaks in the lower frequency bands, whereas in the higher frequency bands large individual differences were observed. Closer inspection of the region where the mu-frequency band could be expected (see Figure 3a) revealed that eight of the twelve participants showed a peak at the central electrode sites around 7.5 or 8.3 Hz. This is in line with previous research, which shows that the power in the mu-frequency band peaks around 8 Hz at the age of 12 months or somewhat below this frequency (Marshall et al., 2002; Stroganova et al., 1999).

To further substantiate the origin of the observed peaks in the spectra, the topographical distribution of the average activity in the mu-frequency band was also plotted (see Figure 3b). This illustrates that the peak of the mu-frequency band showed a broad scalp distribution, and was most prominent at fronto-central electrode sites.

Due to the relatively small number of artifact-free trials, data were collapsed over the Target area conditions for the analysis of the experimental manipulation. Grand averages of the FFTs were calculated for both the Ordinary and Extraordinary conditions. The difference between the grand averages of the two conditions was plotted (see Figure 5). Electrodes of interest, overlying fronto-central sites,

A

B

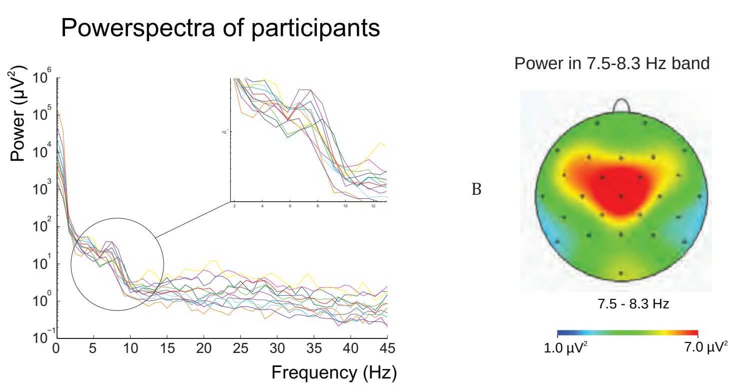

Figure 3: (A) Powerspectra of individual infants averaged over conditions and over the central electrodes. (B) Topoplot displaying the power in the frequency band from 7.5 to 8.3 Hz averaged over all conditions.

were analyzed in a repeated-measures ANOVA with Action Type (Ordinary and Extraordinary) as within-subjects factor.

Results

Visual anticipations to the target areas

First, it was investigated whether infants showed anticipatory looks to the target area of the actions they observed and whether the frequency of anticipatory looks differed between ordinary and extraordinary action movies. The mean percentage of visual anticipations anticipations to the mouth was 27.2 % (*SD* = 9.1) in the Ordinary Mouth condition and 27.2% (*SD* = 21.2) in the Extraordinary Mouth condition (see Figure 4a). Anticipations to the ear occurred less frequently (see Figure 4b). For the Ordinary Ear condition, anticipatory looks towards the ear were observed in 2.0% (*SD* = 6.2) of the attended trials; for the Extraordinary Ear condition, visual anticipations towards the ear were observed on average in 4.1% of the cases (*SD* = 3.7). A 2 × 2 repeated-measures ANOVA was conducted on trials in which the infant attended to the action, with Action Type (Ordinary vs. Extraordinary action) and Target area (Mouth vs. Ear) as independent factors and as dependent variable the frequency of anticipation. The analysis yielded a main effect of Target area, with more frequent anticipations to the mouth compared to

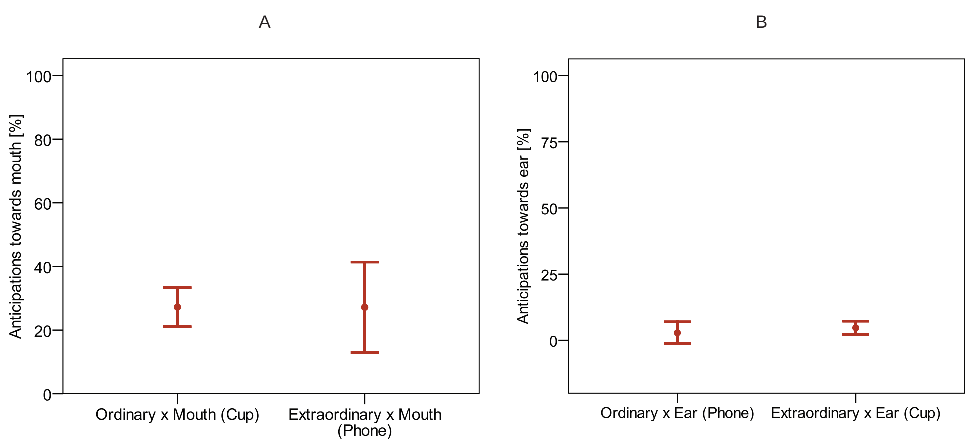

Figure 4: Frequency of visual anticipations. (A) The percentage of anticipatory looks to the mouth in the stimuli with the target area Mouth for Ordinary (left line) and Extraordinary actions (right line). (B) The percentage of anticipatory looks to the ear in the stimuli with the target area Ear for Ordinary (left line) and Extraordinary actions (right line).

the ear, $F(1, 10) = 59$, $p < .001$, Greenhouse-Geisser corrected). No other significant effects were found.

When comparing the latencies of anticipatory eye movements, infants showed no difference between the Ordinary ($M = -117$ ms; $SD = 300$) compared to the Extraordinary ($M = -140$ ms; $SD = 309$) action condition, $t(10) = 25$, $p = 0.8$.

Mu-suppression in the EEG signal during action observation

It was the aim of this study to examine whether the EEG signal in the mu-frequency range was more strongly suppressed during observation of ordinary actions compared to extraordinary actions. Therefore, the grand average FFT of the Ordinary action condition was subtracted from the grand average FFT of the Extraordinary action condition. For the frequencies of interest (7.5 to 8.3 Hz), infants showed a stronger desynchronization in the Extraordinary action condition compared to the Ordinary action condition and this effect was most pronounced over fronto-central sites (see Figure 5). The power in the mu-frequency band measured at these fronto-central electrodes was used as a dependent variable in a repeated-measures ANOVA with Action type (Ordinary vs. Extraordinary action), Hemisphere (Left vs. Right), and Front-to-Back (F3–F4, FC1–FC2, C3–C4) as within-subjects factors. A main effect of Action type was found, $F(1, 11) = 5.9$, $p = .04$, Greenhouse-Geisser corrected, with lower power in the Extraordinary action

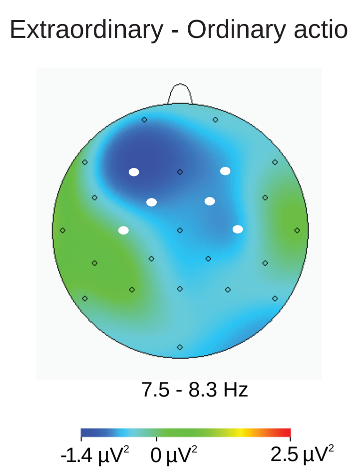

Figure 5: Topoplot displaying the difference in power between the Extraordinary and the Ordinary action conditions in the frequency band from 7.5 to 8.3 Hz. The white dots indicate the electrodes that were included in the analysis.

condition (M = 5.4 μV²; SD = 2.9) compared to the Ordinary action condition (M = 6.3 μV²; SD = 3.7). No other main effects were found. Moreover, there were no significant interactions, which suggests that the effect was evenly distributed over both hemispheres.

Discussion

This study investigated how infants perceive ordinary and extraordinary actions and examined the role of motor activation during the processing of these actions. Infants observed object-directed actions: A cup and a phone were brought either to the ordinary target location (cup to mouth; phone to ear) or to an unusual target location (cup to ear; phone to mouth). Infants showed stronger motor activation during the observation of extraordinary compared to ordinary actions, as reflected in a stronger desynchronization of the mu-frequency band of their EEG. These results suggest that the infants' motor system is involved in processing observed actions, but more importantly, their motor system seems to respond differently for ordinary and extraordinary actions.

When watching the stimulus movies, the infants in our study showed visual anticipations to the target area of the ongoing action. This is in line with the findings of Hunnius and Bekkering (2010), who found that infants from 6 months of age on display predictive looks to the target area of actions they observe. In their study, ordinary actions led to more frequent anticipatory looks than extraordinary actions. In the current study, however, no significant difference was found in the frequency of anticipatory looks. Infants showed predictive looks about as frequently for the ordinary as the extraordinary actions, which might be due to the fact that they learned about the unfamiliar object–target associations as a consequence of the large number of stimulus repetitions. Indications of learning effects had been present in the original study of Hunnius and Bekkering (2010), but less pronounced. In the current study, learning might have had a stronger effect, as EEG experiments require far more trials than eye-movement studies. In this EEG experiment, infants were presented with up to 30 repetitions of each action compared to a maximum of 9 in the eye-tracking study of Hunnius and Bekkering (2010).

The current study was designed to study the neural correlates that distinguish ordinary actions from extraordinary actions. As mentioned before, desynchronization in the mu-frequency band reflects motor activation (Gastaut & Bert, 1954; Muthukumaraswamy et al., 2004). Though in the current study the mu-frequency desynchronization during action observation appeared rather frontal, similar scalp-distributions of motor related effects have been found before (see, e.g., van Elk, van Schie, Zwaan & Bekkering, 2010; Pfurtscheller, Brunner, Schlögl, & Lopes da Silva, 2006; displaying individual variation in topoplots in mu-frequency desynchronization). Furthermore, in our study, the power in the mu-frequency band averaged over all conditions was found maximal at frontocentral sites.

When comparing brain responses to extraordinary actions and ordinary actions, we found a stronger desynchronization in the mu-frequency band during perception of extraordinary actions. The finding that infants respond differently for actions with uncommon end states is in line with the literature. Infants appear to have expectations about the end state of other people's actions at early ages. For instance, when confronted with an action end state which deviates from the visual pattern, infants display longer looking times (see e.g., Phillips et al., 2002; Reid et al., 2007; Woodward, 1998). Furthermore, as previously mentioned, infants have been shown to visually anticipate to the target area of observed actions (Falck-Ytter et al., 2006; Hunnius & Bekkering, 2010). In addition to this behavioral evidence, a number of developmental neuroimaging studies show findings in line with our results that infants have expectations about how actions they observe should end. Reid and colleagues (2009), for instance, showed that 9-month-old infants differentiate between ordinary and extraordinary action end states. Infants displayed an N400-like pattern when observing an extraordinary action end state, which indicates that their expectations as to how the action would end were violated. Moreover, infants appeared to notice if an action was stopped before its goal had been reached, as indicated by more gamma-activity over left frontal regions during observation of incomplete actions (Reid et al., 2007).

Previous research has thus demonstrated that infants make predictions about end states of actions they observe. However, which processes underlie these predictions has not been established to date. The present study is in line with the notion that the motor system might play a role in action prediction (see e.g., Kilner et al., 2007; Prinz, 2006; Wolpert & Flanagan, 2001; Schütz-Bosbach, & Prinz, 2007). According to the predictive coding framework (Kilner et al., 2007), actions that develop differently than expected beforehand should elicit stronger motor activation, because the predictions need to be updated to match the predicted visual scene with the actual visual input. Our results are compatible with this framework, as the infants showed stronger motor activation during observation of extraordinary actions compared to ordinary actions. Moreover, the difference in motor activation occurred during the lifting movement of the object, so while the action was still unfolding. The timing of this effect corresponds with the time-window in which one would expect the motor system to be at work to generate predictions about how the action will develop and how it will end. Importantly, the effects in the mu-frequency band cannot be attributed to differences in overt eye movements, because no quantitative differences were found between the visual anticipations in the two conditions.

Consistent with our findings, recent empirical research with adults has shown that the observation of actions that deviate from what participants would normally have expected is associated with stronger motor resonance. Koelewijn and colleagues, for instance, found a stronger desynchronization in the beta-frequency band originating from motor areas while participants were watching actions that were clearly mistakes compared to correct actions (Koelewijn, van Schie, Bekkering, Oostenveld, & Jensen, 2008). This modulation of the beta-band might reflect a stronger motor activation in response to deviant action stimuli. Also, Manthey, Schubotz, and von Cramon (2003) describe a stronger motor activation when participants were watching movements that differed from what one would expect *a priori* (e.g., unlocking a bicycle lock with the key held transverse to the lock). Similarly, a recent fMRI study using pictures of extraordinary compared to ordinary action end states demonstrated a stronger activation of the inferior frontal gyrus (IFG), which is part of the frontal parietal motor network (de Lange, Spronk, Willems, Toni, & Bekkering, 2008). Comparable results come from neuroimaging studies that investigated neuronal responses to action language. In adults, processing of sentences and action pictures describing unfamiliar action scenarios is associated with stronger motor activation compared to sentences and action pictures of familiar action scenarios (Beilock, Lyons, Mattarella-Micke, Nusbaum, & Small, 2008 [fMRI, sensorimotor areas]; van Elk et al., 2010 [mu-frequency effect, fronto-central sites]). In sum, these studies provide converging evidence that in adults, motor resonance tends to be stronger for the perception of unusual actions.

Although motor processes are thought to play an important role in human action prediction, there are of course other ways to predict action end states (Rizzolatti & Sinigaglia, 2010; de Lange et al., 2008). In the infant domain, two more mechanisms have been suggested to support action understanding and action prediction (for an overview, see Csibra & Gergely, 2007). First, it has been put forward that young infants evaluate actions they observe on the basis of abstract cognitive principles of rationality (Gergely & Csibra, 2003). Following this account, infants infer action goals on the basis of the observed action path and the situational constraints. Second, infants might learn about others' actions and intentions through repeated observation of actions, as they couple actions to their effects (Elsner & Aschersleben, 2003). These three mechanisms—rationality, action–effect associations, and motor activation—are likely to complement and support each other. Also in the current study, infants might have formed action–effect associations that helped them to make predictions about the course of the actions they observed. The stimulus presentation we used supported the formation of such associations, as for instance the different action types (ordinary vs. extraordinary) were carried out by different actors and as a blocked design was used with 10 repetitions of the same action type in a row. This experimental design provided the infants with a maximal chance to make correct predictions of the action end state for both ordinary and extraordinary actions. Although the design allowed the infants to acquire action–effect associations, this cannot account for the difference we found between ordinary and extraordinary actions. That is, learning opportunities for action–effect associations were comparable for ordinary and extraordinary action conditions (i.e., one actor performed ordinary actions; another actor always extraordinary actions), but still, a stronger activation of motor-related brain areas was found for extraordinary compared to ordinary actions. This motor activation might be a reflection of the predictions generated by the motor system. Extraordinary actions required additional predictions to be generated to infer the action end state, resulting in a stronger motor activation during perception of extraordinary actions. Our data thus suggest that the motor system is involved in action prediction and making sense of others' actions from early on, and might be even more fundamental for cognition than previously thought.

Acknowledgements

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Chapter 3

Online Prediction of Others' Actions: the Contribution of the Target Object, Action Context and Movement Kinematics

Abstract

Previous research investigated the contributions of target objects, situational context and movement kinematics to action prediction separately. The current study addresses how these three factors combine in the prediction of observed actions. Participants observed an actor whose movements were constrained by the situational context or not, and object-directed or not. After several steps, participants had to indicate how the action would continue. Experiment 1 shows that predictions were most accurate when the action was constrained and object-directed. Experiments 2A and 2B investigated whether these predictions relied more on the presence of a target object or cues in the actor's movement kinematics. The target object was artificially moved to another location or occluded. Results suggest a crucial role for kinematics. In sum, observers predict actions based on target objects and situational constraints, and they exploit subtle movement cues of the observed actor rather than the direct visual information about target objects and context.

Keywords: Action prediction, Context, Object, Kinematics

Based on: Stapel, J.C., Hunnius, S., & Bekkering, H. (2012). Online prediction of others' actions: the contribution of the target object, action context and movement kinematics. *Psychological Research, 76*, 434-445.

Introduction

From very early in life, humans do not only just passively observe other people's actions but also predict their action goals while watching the actions unfold (see e.g., Falck-Ytter et al., 2006; Stapel, Hunnius, van Elk, & Bekkering, 2010; Hunnius & Bekkering, 2010). Predicting others' actions is essential in understanding the other (Blakemore & Decety, 2001), and allows us to smoothly interact with each other (Sebanz, Bekkering, & Knoblich, 2006). When observing actions, there are several sources of information which can form the basis of these predictions. Goal objects, together with situational constraints, the actor's movement kinematics, and the action path itself, together make up an action (Cuijpers, van Schie, Koppen, Erlhagen, & Bekkering, 2006). Although it is clear that all these factors might affect action prediction, they have to date never been examined together in one empirical study. Especially the role of movement kinematics in combination with other (competing or confirming) information is unclear. That is, on the one hand, it is obvious that there is a "tight coupling between kinematics and goals" (Grafton & Hamilton, 2007, p.609), on the other hand, both behavioral (Bach, Knoblich, Gunter, Friederici, & Prinz, 2005; van Elk et al., 2008a) and neuroimaging data (Grafton & Hamilton, 2007) suggest goals to be more prominent than movement kinematics in action perception. The current study is the first to investigate the role of goal objects, environmental constraints, and movement kinematics for predictions about the action path of an observed actor.

How people come to predict others' actions has been studied with different paradigms, all contributing pieces to the puzzle of which sources in the visual domain may be used for these action predictions. In general, empirical studies mainly have explored how these sources contribute to action prediction in isolation. Theoretical models, on the other hand, have to some extent focused on combined sources for action prediction, as they all incorporate contextual constraints and goals as major factors. According to Gergely and Csibra (2003) and Baker, Saxe, and Tenenbaum (2009), humans predict actions of intentional agents by assuming that they take the most efficient path to get to a certain goal. The presence and position of environmental constraints, such as barriers, determine which path is most efficient for the agent to take. Hence, one can predict the action path based on information about the goal of an action and the action constraints. Some models include movement kinematics as a third factor explaining action prediction, besides goal and action constraint information (see e.g., Cuijpers et al., 2006; Kilner et al., 2007). According to Kilner et al. (2007), action predictions are generated by the mirror neuron system (MNS), and are based on information from observed movement kinematics (lowest level), goal inferences (highest level), and contextual information (serving as a prior). Taken together, three aspects are mentioned in the literature which can underlie action predictions, namely information about goals, context and movement kinematics.

The contribution of all three factors in isolation to action perception is indicated by several empirical studies. First of all, contextual information can help in assessing and predicting an action goal. The same hand posture can be interpreted as having the action goal “to clean up” or “to drink”, based on a different context in which the hand is displayed, and the inferior frontal gyrus (which is suggested to be part of the human MNS, see also Rizzolatti & Craighero, 2004) responds differently in these two cases (Iacoboni et al., 2005). The presence or absence of contextual constraints, such as obstacles, can lead to different predictions about an action path. For instance, infants’ expectations seem violated when an agent makes a detour which is no longer ‘needed’, because, an obstacle is removed from the scene (Gergely et al., 1995; but see: Paulus et al., 2011c). Adults also seem to take action constraints into account when making predictions about which goal location an agent is heading for (Baker et al., 2009).

Second, goal objects and locations have been shown to have a considerable impact on action prediction. Observing objects which can function as an action goal leads to predictions about what action will follow (see e.g., Tucker & Ellis, 2004). Furthermore, when viewing objects and associated actions, observers generate predictions about goal locations (van Elk, van Schie, & Bekkering, 2009; Hunnius & Bekkering, 2010). Moreover, results from neuroimaging studies illustrate that observed object-directed actions are processed differently in the brain than intransitive actions. For instance, observation of object-directed actions leads to stronger effects in cortical motor areas than non-object-directed actions (Muthukumaraswamy et al., 2004; Buccino et al., 2001; Caspers, Zilles, Laird, & Eickhoff, 2010). Furthermore, observation (and simulation) of object-directed actions is tends to activate different regions in the parietal lobe compared to intransitive actions (Jeannerod, 1994; Lui et al., 2008; Creem-Regehr & Lee, 2005).

Third, action kinematics can be used in understanding and predicting the observed actions. For instance, participants can judge based on body movements of actors whether the weight they lift corresponds to the weight they expect (Grèzes, Frith, & Passingham, 2004a), and whether lifting a certain weight was pretended or real (Grèzes, Frith, & Passingham, 2004b). Furthermore, the intention underlying a grasping movement (to cooperate, compete or to perform an individual action) can be accurately predicted when the start of this movement is observed (Sartori et al., 2011). Even when the action seems to have no target object, accurate predictions about an observed action can be made on-line when watching movement kinematics (Graf et al., 2007). Predicting the flow of these observed movement kinematics is easier when an observed point-light figure displays human kinematics compared to less complex non-human kinematics, which suggests that the motor system maps observed actions to come to predictions of the observed action (Stadler, Springer, Parkinson, & Prinz, 2012). In addition, in real life tasks, such as in joint action settings, people not only predict the goal of another person's action but also the action kinematics necessary to achieve this goal. This is illustrated by the finding that people adjust their behavior such that beginning state comfort is attained for an interaction partner (Gonzalez, Studenka, Glazebrook, & Lyons, 2011).

In sum, previous research demonstrates that contextual constraints, goal objects as well as action kinematics can be used for action prediction. However, how these three aspects together contribute to action predictions of human actions remains unclear. Especially, the role of movement kinematics opposed to more abstract object and context information needs further investigation. Theoretically, action predictions could be solely based on the combination of situational constraints and target objects. However, when simulating an observed action, movement kinematics may also play a role in the prediction how an observed action will unfold. The current research question, thus, was two-fold. Do people take situational constraints and target objects into account when predicting how an observed ongoing action will unfold? And if so, do they at least partially rely on the movement kinematics in making their predictions? Experiment 1 was designed to answer the first question. There, predictions had to be made about the subsequent movement of an observed actor, while the action was object-directed or not, and was constrained by the context or not. Experiment 2A and 2B allowed us to examine whether predictions were made purely on the information about the goal object in combination with the context of the action, or whether the predictions were based on the actor's movement kinematics. The previous work in the area of action observation suggests that action representations are hierarchically organized (Grafton & Hamilton, 2007), such that incongruent information from means is less detrimental than incongruent goal information when processing observed actions (van Elk et al., 2008a). In similar fashion, we provided participants in Experiment 2A with movement kinematics which were incongruent with the goal-object and action context. Different theories would generate opposing hypotheses for this conflict in provided information. If action predictions are mainly based on goal-objects and situational constraints, prediction accuracy may show a similar pattern as in Experiment 1. On the other hand, if humans make use of all three sources of information (goal-object, action context, and kinematics) for their action predictions, conflicting information may lead to reduced differences between the conditions. However, if kinematics are driving action prediction, the pattern in the prediction accuracy data of Experiment 1 might be reversed. In Experiment 2B, information about the goal object was no longer available to the participant. If action predictions are mainly based on goal-objects and action context, one would expect to find a main effect of action context, and no effect of object-directedness. Alternatively, when movement kinematics can be used as a basis for action prediction, a more elaborate pattern of accuracy data may be obtained.

Experiment 1

METHOD

Participants

Eighteen participants (3 males) with a mean age of 22 years (SD = 4 years) were tested. They gave written informed consent to participate and either chose to receive five euros in vouchers for participation or credit points. All were right-handed students recruited at the Radboud University in Nijmegen.

Design

The study was an action-observation setting, in which a two by two within-subjects design was applied. Participants viewed videos of an actor walking a few steps and then crawling. In half of the cases the action was object-directed, in the other half it was not-object-directed (Target object vs. No target object). As a second manipulation, the action context was manipulated such that crawling took place either underneath the table or beside the table (Underneath table vs. Beside table). Halfway the second step of the actor, the video was paused and participants had to judge whether the actor would take another step walking or change to crawling. In 50% of the cases, the correct response would be that the observed actor would start crawling. Responses were given by pressing one of the two response-buttons with the left or right index finger. Between subjects, the response buttons were counterbalanced between left and right hand. Accuracy rate of the responses (correct/incorrect) and the d prime (*d'*) of this accuracy rate were the dependent variables.

Materials

Stimuli were videos which displayed three different female actors standing still for one second, then starting to move with two or three steps walking and then crawling in the same direction, and ending with a still posture of approximately one second. Average stimulus duration was 5.7 s (SD = 0.4 s). Stimulus movies were presented with a frame rate 25 frames per second, were displayed against a black background and were 408 pixels high and 720 pixels wide. In all videos, a table and a volley ball were present. The ball lay either on the floor (Target object condition) or on the table (No target object condition). As participants received the information that the actor would first walk and then crawl, it was clear from the start of the experiment that the action was not object-directed if the ball lay on the table. The table stood in front of a white wall. The actor either moved close to the wall (see Fig. 1a), or a few steps more in front (see Fig. 1b), which made clear from the start of the movie whether the actor would crawl underneath the table (close to the wall) or beside the table (a bit more in front). When video-taping the actions, stimuli were recorded mixing the order of conditions constantly, such that differences in the movements of the actor are not a consequence of having repeated the exact same action in the same context repeatedly. Actors were trained in making stimulus material, and were instructed to act as similar as possible in all their actions. To ensure the similarity between the stimuli, actors were shown example videos before and in-between taping sessions, and were asked to pay special attention to their walking pace, how to end the action in a natural fashion, and the shift from walking to crawling. For each condition, ten different stimuli were used. The stimuli displayed three different actors. However, one of the actors moved in a different way than the other two. That is, she had the tendency to not walk upright, and she moved both her hands before her body when starting to crawl. Nevertheless, her stimulus movies were included to keep some natural variation in the stimuli, but only in two out of every ten stimuli per condition. Furthermore, the movement direction was varied, and between stimuli, there were little changes in the position of the furniture, starting position of the actor, and position of the ball. This was to ensure that exact timing and position of crawling of the actor could not be inferred from having seen the other stimuli. Stimuli were between conditions matched for stimulus duration, movement duration, position of the table, movement direction (left or right), amount of steps before crawling and the horizontal distance to the ball. For all stimuli, the motion energy for the complete videos as well as for the part of the videos before the pause was calculated. Motion energy can be indicative for differences in movements contained

Figure 1a: Example frame in which actor will start crawling.

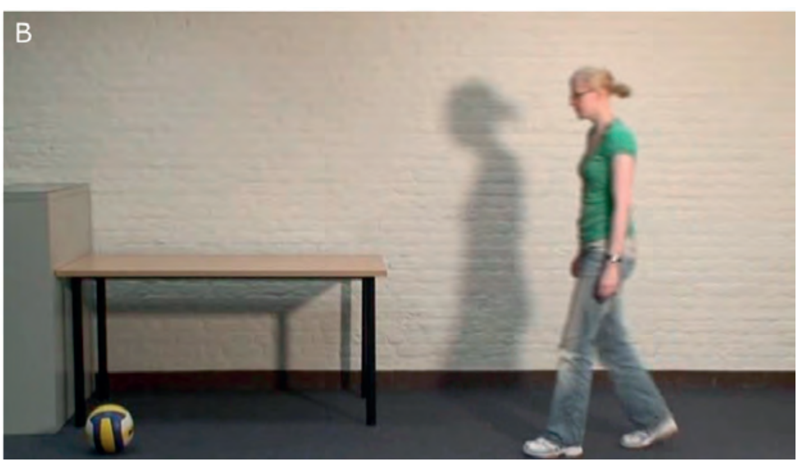

Figure 1b: Example frame in which actor will continue another step walking.

in videos (Bobick, 1997; Schippers, Roebroeck, Renken, Nanetti, & Keysers, 2010). Between subjects ANOVAs were conducted to test for differences in the variability (expressed as the SD of the motion energy in the videos) of motion in the movies, with context and object-directedness as explanatory variables. Both ANOVAs showed a main effect of context [Until the pause: $F(1,36) = 4.4$, $p = 0.04$; Complete videos: $F(1,36) = 82$, $p < 0.001$], with larger SDs in the motion energy for the beside table condition (Until pause: M = 2,890,012; Complete videos: M = 3,286,818) compared to the Underneath table condition (Until pause: M = 2,397,975; Complete videos: M = 2,241,175). The motion-energy algorithm applied here is the sum of the squared differences in the color channels of each pixel between frames (cf. Schippers et al., 2010). In the Beside tables conditions the actor moves closer to the camera, and takes up a larger area, and hence more pixels, of the stimulus, which could explain the results of the motion energy ANOVAs. Alternatively, it might be that the actors move in a less-variable manner in the Underneath table condition compared to the Beside table condition.

All conditions consisted of 10 different stimuli which were each repeated four times during the experiment. Stimuli were presented in random order. To slow down unwanted habituation effects, we included 15 catch trials (8% of the trials) in which the action path differed from the usual path (e.g., crawling on the table, walking beside the table).

The experiment was conducted using a custom-made stimulus presentation and data registration program implemented in Presentation 13.1 (Neurobehavioral Systems, CA, USA). A response-button box was used to log the responses of the participants.

Procedure

The experiment started with an instruction phase, in which participants learnt that the stimuli would display an actor who would walk and then crawl. Furthermore, the stimuli would be paused after several steps of the actor, followed by a question: "Will the actor now start crawling, or will she take another step walking?" (see Fig.1a and b for example frames at which the videos were paused). Participants were instructed to respond as fast and accurate as possible. After their response, the rest of the video would be displayed. Participants practiced with two example stimuli and were provided with feedback about the accuracy of their response. During the actual experiment, no explicit feedback was given, although it could be inferred from watching the rest of the stimulus movie. In total, the experiment took about 30 min to complete. After finishing the experiment, participants were thanked and received participation vouchers or credit points.

RESULTS

For each participant, the accuracy rate per condition was calculated. Furthermore, mean *d*' per participant per condition was calculated (see Table 1).

Table 1. Mean accuracy rates and *d*' per condition for Experiment 1, 2A, and 2B. Standard deviations are noted between brackets.

	Exp.1		Exp. 2A		Exp. 2B	
	Accuracy rate	*D prime*	Accuracy rate	*D prime*	Accuracy rate	*D prime*
Underneath table x Target object	73% (8.6)	1.36 (0.64)	57% (12)	0.30 (0.60)	74% (11)	1.48 (0.74)
Underneath table × No target object	55% (7.0)	0.26 (0.38)	70% (11)	1.29 (0.71)	54% (11)	0.15 (0.57)
Beside table x Target object	57% (7.0)	0.24 (0.44)	59% (8)	0.59 (0.60)	56% (5.8)	0.12 (0.37)
Beside table x No target object	56% (7.2)	0.42 (0.49)	55% (10)	0.06 (0.63)	61% (9.0)	0.75 (0.16)

A two-by-two repeated measures ANOVA was conducted with Object-directedness and Context as independent factors, and accuracy rate as dependent variable. A main effect of Context [$F(1,17) = 12.8$, $p = 0.002$], a main effect of Object-directedness [$F(1,17) = 78.8$, $p < 0.001$] as well as the interaction between these two factors [$F(1,17) = 25.2$, $p < 0.001$] were found to be significant. Post hoc paired-samples t-tests revealed that accuracy rates were significantly higher in the Underneath table conditions (M = 64%) than in the Beside table conditions [M = 56%, $t(17) = 3.6$, $p = 0.002$]. Furthermore, the Target object conditions yielded a significantly higher prediction accuracy rates (M = 65%) than the No target object conditions [M = 55%, $t(17) = 8.9$, $p < 0.001$].

As Fig. 2 reveals, the main effects are driven by the interaction effect, which reflects the significantly higher accuracy rates in the condition Underneath table with Target object condition compared to all other conditions [all comparisons with the Underneath table with Target object condition: $t(17) > 5.8$, $p < 0.001$; $t(17) < 0.8$, n.s. for all other comparisons]. The *d*' analysis showed exactly the same pattern of results, with again a significant main effect of Context [$F(1,17) = 17.1$, $p < 0.001$], a significant main effect of Target object [$F(1,17) = 42.8$, $p < 0.001$], and a significant interaction effect of these two factors [$F(1,17) = 30.5$, $p < 0.001$], when

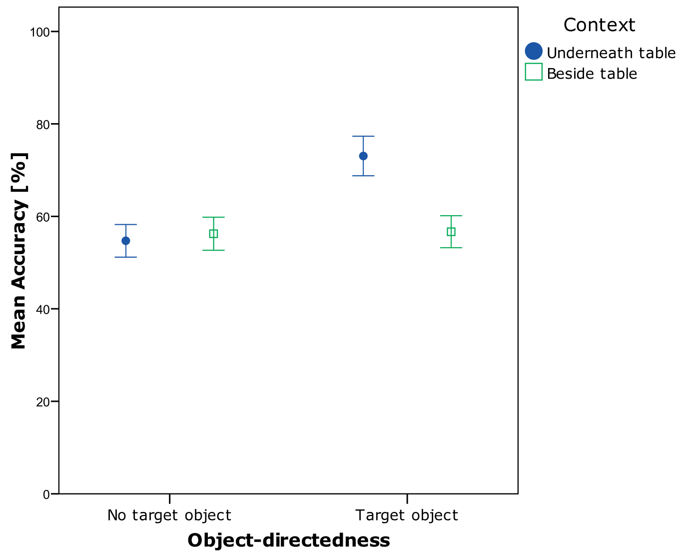

Figure 2a: Mean accuracy per condition Exp. 1. Bars represent 95% confidence intervals of SE.

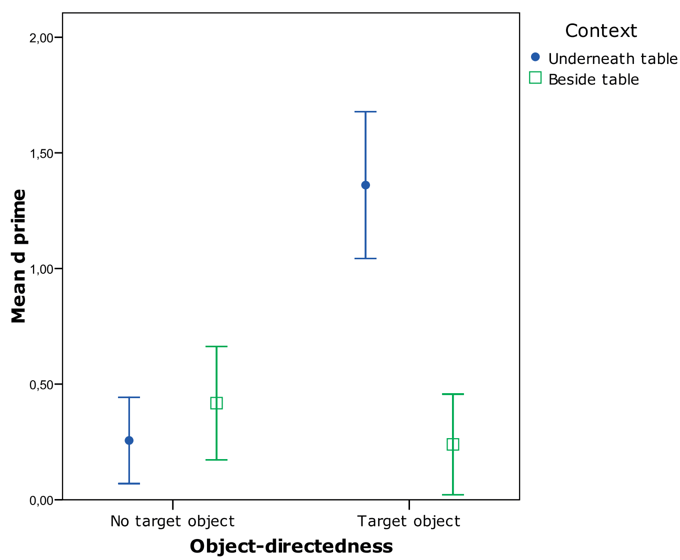

Figure 2b: Mean d' per condition Exp. 1. Bars represent 95% confidence intervals of SE.

applying a two by two repeated measures ANOVA. Post hoc paired-samples t-tests investigating the two main effects, show that the *d*'s were higher in the Underneath table (M = 0.81) compared to the Beside table conditions [M = 0.33; $t(17) = 4.1$, $p = 0.001$], and that the *d*'s of the Target object conditions (M = 0.80) were higher than the No target object conditions [M = 0.34; $t(17) = 6.5$, $p < 0.001$]. These two main effects are explained by the interaction effect, with significantly higher *d*'s in the condition Underneath table with Target object compared to all other conditions [all comparisons with the condition Underneath table with Target object: at least $t(17) > 6.6$, $p < 0.001$; $t(17) < 1.6$; n.s. for all other comparisons].

CONCLUSION

The data of Experiment 1 show that participants' predictions of the next move of an actor were more accurate when two things hold: the action was object-directed and contextually constrained compared to the other three combinations. To rule out the possibility that the effect found was a response bias, i.e., participants have a general tendency to react more often with a positive response when the action is object-directed, *d*'s were calculated. *D*' is a measure originating from the sensory detection theory. It is the difference between the z-score of the hit rate and the z-score of the false alarm rate (Macmillan & Creelman, 1991). The larger this difference, the more sensitive is the measure it reflects. The *d*' analysis yielded the same pattern of results as the accuracy data, showing that the results are not a mere response bias. Furthermore, this suggests that participants become more sensitive in their predictions when there is a target object and the context of the action constrains the actor.

The finding that the accuracy of action predictions in all three other conditions did not differ from each other, suggests that the effect of context and target object are not independent from each other. Apparently, a contextually constrained movement only becomes more predictable if a target object is present. The target object might direct the movements of the actor towards a specific location, which renders the movement more predictable. However, the presence of the target object in itself is apparently not enough to inform the observer about the exact timing of crawling onset of the actor. To predict whether crawling will start immediately after the pause or not, more information seems needed. This information is provided by the contextual constraint. That is, the constraint induces a spatial restriction on the spacing and timing of the transition from walking to crawling, which may increase the predictability of the action. Consequently, the combination of object-directedness and action constraints might lead to more accurate predictions.

From this experiment, it cannot be concluded whether the predictions made are the product of the combination of the goal and context information given by the visual scene, or are possibly derived from the movements of the actor. Therefore as a follow-up, the videos were edited in such a fashion that the target object was placed on a different location in the scene. Consequently, the movement kinematics of Experiment 1 were preserved, but the target information was shifted. Stimulus movies in which there used to be a target object lying on the floor were rendered into movies in which the target object was now lying on the table. The opposite was done with the stimulus movie in which there used to be no action target (as the object had been lying on the table without any function). Here, the object now became the target of the movement (the movie was edited in a way that the object was now lying on the floor). If the most accurate action predictions would still be found in the new Underneath table with Target object condition, this would provide evidence for a role of target information in action prediction. Furthermore, this would show that movement kinematics are neglected by observers when making predictions about an ongoing action, and that situational constraints and target objects are the cornerstones of action prediction (Gergely & Csibra, 2003; Baker et al., 2009). However, if the effect would now be found in the new Underneath table with No target object condition (with the kinematics of the previous Underneath Table with Target object condition), this would support the notion that movement kinematics play a role in action predictions.

Experiment 2a

METHOD

Participants

Twenty-eight students (4 males) of age 21 years (SD = 2 years) participated in the study and chose to receive either five euros in vouchers or credit points for participation. All gave written informed consent and were right handed students recruited at the Radboud University in Nijmegen. One participant was excluded from analysis because of computer problems.

Design

The same design as in Experiment 1 was applied.

Materials

The same stimulus material as in Experiment 1 was used as the basis for Experiment 2. However, all stimulus videos were edited offline beforehand using Adobe Premiere CS 4 (CA, USA). The target object was placed on a different location in the scene. In the Underneath table with Target object movies, the ball was placed on the table, rendering it into an Underneath table with No target stimulus. In the Underneath table with No target condition, the opposite was done: the ball was now placed underneath the table. In a similar fashion, stimuli of condition Beside table with Target object were transformed into Beside table with No target and vice versa (by placing the ball either on the table or on the floor beside the table). Besides the editing of the stimulus materials, no changes were made to the experiment.

Procedure

The same procedure was applied as in Experiment 1.

RESULTS

As in Experiment 1, accuracy rates and *d*'s were calculated per condition per participant (see Table 1). A two (Context) by two (Object-directedness) repeated measures ANOVA revealed that accuracy rates were influenced by both factors [Context: $F(1,26) = 11.6$, $p = 0.002$; Object-directedness: $F(1,26) = 9.9$, $p = 0.004$] and by the interaction of the two [$F(1,26) = 29.4$, $p < 0.001$]. Accuracy rates were significantly higher in the Underneath table conditions (M = 63%) compared to the Beside table conditions [M = 57%; $t(26) = -3.1$, $p = 0.004$]. The No target object conditions resulted in more accurate action predictions (M = 63%) than the Target object conditions [M = 58%; $t(26) = 3.4$, $p = 0.002$]. Figure 3a demonstrates that the main effects found were a consequence of the significantly higher accuracy rates when the actor crawled underneath the table with no target compared to the other three conditions [$t(26) > 5.2$, $p < 0.001$ for all comparisons with the Underneath table with No target condition; $t(26) < 1.8$, n.s. for all other comparisons].

An equivalent repeated measures ANOVA was run on the *d*' data and yielded the same pattern of results, namely again two main effects [Context: $F(1,26) = 18.9$,

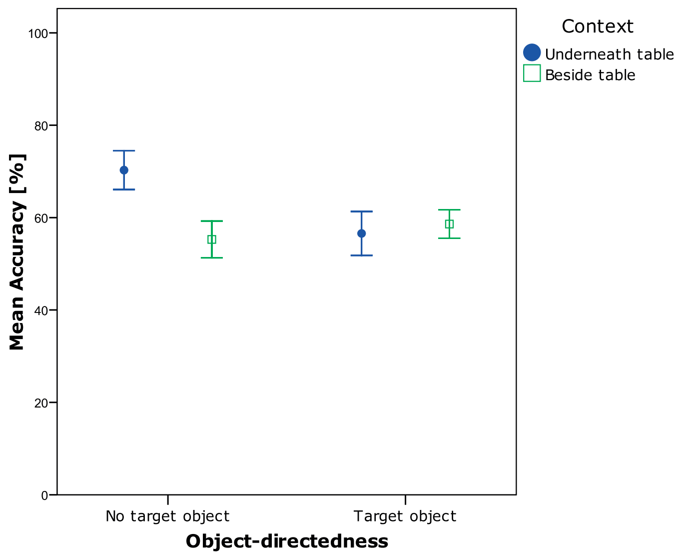

Figure 3a: Mean accuracy per condition Exp. 2A. Bars represent 95% confidence intervals of SE.

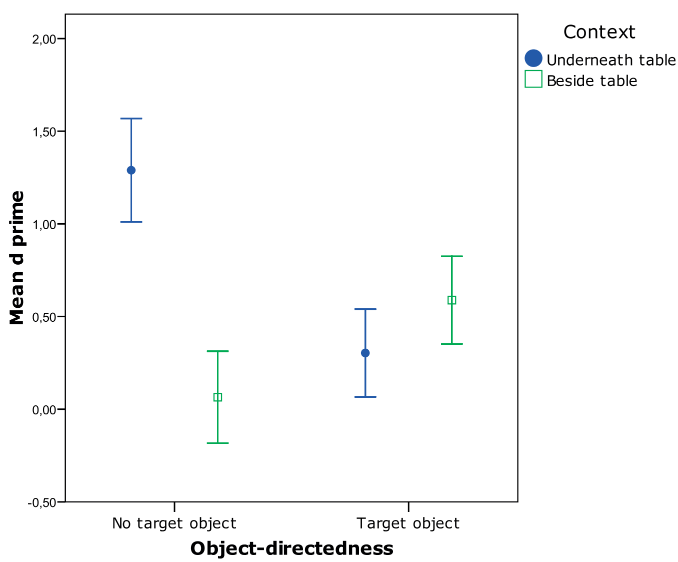

Figure 3b: Mean *d*' per condition Exp. 2A. Bars represent 95% confidence intervals of SE.

$p < 0.001$; Target object: $F(1,26) = 5.0$, $p = 0.03$] and interaction effect [$F(1,26) = 51.6$, $p < 0.001$]. Post hoc paired-samples t-tests, investigating the two main effects, reveal that the *d*'s were higher in the Underneath table (M = 0.80) compared to the Beside table conditions [M = 0.33; $t(26) = 4.4$, $p < 0.001$], and that the No target object conditions yielded higher *d*'s (M = 0.68) than the Target object conditions [M = 0.45; $t(26) = -2.2$, $p = 0.03$]. The two main effects and the interaction effect in this ANOVA could be explained by significantly higher *d*'s (M = 1.29) for the condition in which the crawling took place underneath the table with no target object compared to the three other conditions [highest other: $M_{Besides\_table\_x\_Target\_object} = 0.59$. Comparisons with Underneath table with No target condition were significant: all *t*'s(26) > 4.7, $p < 0.001$]. Other post hoc paired-samples t-tests showed that although *d*'s appeared to be higher in the Beside table with Target object condition, this was not a systematic difference [comparison with Beside table with No target: $t(26) = 4.1$, $p < 0.001$; comparison with Underneath table with Target object: $t(26) = 1.9$, n.s.].

CONCLUSION

Results of Experiment 2A show a difference in the accuracy of action predictions between conditions. Participants performed significantly better if the action was constrained by the context and not object-directed. The *d*' analysis yielded the same pattern of results, indicating that the effect in the accuracy data is not a mere response bias. Action predictions were more accurate for the stimuli which were in the first experiment object-directed and contextually constrained. Thus, the effect found in Experiment 1 shifted together with the original movement kinematics. This finding suggests that not the target object itself influences the observers' action predictions, but the movement kinematics of the actor they observed. To further establish this finding, a second manipulation was carried out, in which the target object was not visible in any of the stimuli. This was done by means of an occluder. In this case, the effect could either disappear, indicating that target object information is crucial for action prediction, or it could stay, indicating that movement kinematics help us in making accurate predictions about observed actions.

Experiment 2b

METHOD

Participants

In Experiment 2B, 24 participants (four males) took part with a mean age of twenty years (SD = 2 years). All were right-handed students and gave written informed consent for participation. They were recruited at the Radboud University Nijmegen and received afterwards either five euros in vouchers or credit points for participation. For one subject, data could not be recovered because of computer problems.

Design

The same design as in Experiment 1 and 2A was applied.

Materials

The same stimulus material as in Experiment 1 was used. However, a black occluder was placed over the target object. The dimensions of the occluder were equal for all stimuli, namely 220 pixels wide and 720 pixels high, occluding the right or the left side of the stimulus (depending on the movement direction of the actor), and occluded the target object entirely (see Fig. 4). After the response of the participant, the occluder was removed, showing the complete, original scene. Apart from these changes in the stimulus material, no changes were made to the experiment.

Procedure

The same procedure as in Experiment 1 and 2A was applied.

RESULTS

Comparable to Experiment 1 and 2A, accuracy rates and *d*'s were determined for each participant in each condition (see Table 1). A two by two repeated measures ANOVA showed that Context had a significant impact on the accuracy rates [$F(1,22) = 7.2$, $p = 0.01$], as did the manipulation of the Target object [$F(1,22) = 20.5$, $p < 0.001$], and the interaction between these two factors was also found to be significant [$F(1,22) = 82.9$, $p < 0.001$]. Post hoc paired-samples t-tests were conducted to verify the direction of the main effects. Action predictions were more accurate in

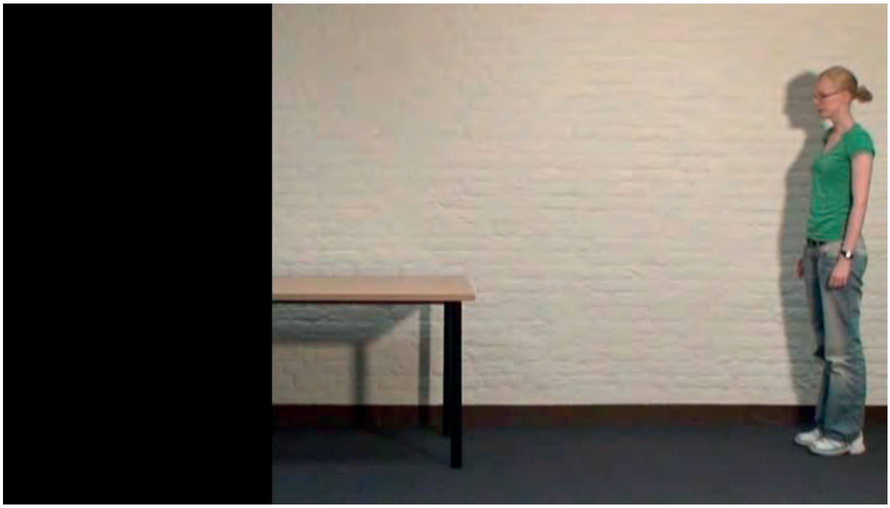

Figure 4: Example of the first frame of a stimulus movie in Experiment 2B.

the Underneath table (M = 64%) compared to the Beside table conditions [M = 58%; $t(22) = 2.7$, $p = 0.01$]. Furthermore, participants responded more accurately when the action had a Target object (M = 65%) compared to when there was No target object [M = 58%; $t(22) = 4.5$, $p < 0.001$]. Additional post hoc paired-samples t-tests were executed to examine the interaction effect. These t-tests show that accuracy rates were highest in the condition where the actor crawled underneath the table towards a target object [all t's(22) > 4.8, $p < 0.001$]. As can also be seen in Fig. 5, accuracy rates in the condition where crawling took place beside the table with no target were also slightly higher than the two remaining conditions [all t's(22) > 3.0, $p <= 0.006$]. This effect was driven by the stimuli of one specific actor, who acted only in two out of ten movies per condition.

The two by two repeated measures ANOVA on the d's, again mirrors the results of the accuracy data, with a main effect of Context [$F(1,22) = 10.4$, $p = 0.004$], a main effect of Target object [$F(1,22) = 12.1$, $p = 0.002$], and a significant interaction [$F(1,22) = 109$, $p < 0.001$]. Post hoc paired-samples t-tests were conducted to investigate the two main effects. The Underneath table conditions appeared to have higher d's (M = 0.82) than the Beside table conditions [M = 0.43; $t(22) = 3.2$, $p = 0.004$]. Furthermore, the Target object conditions yielded more sensitive action predictions (M = 0.80) than the No target object conditions [M = 0.45, $t(22) = 3.5$, $p = 0.002$]. To study the interaction effect, paired-samples t-tests were conducted

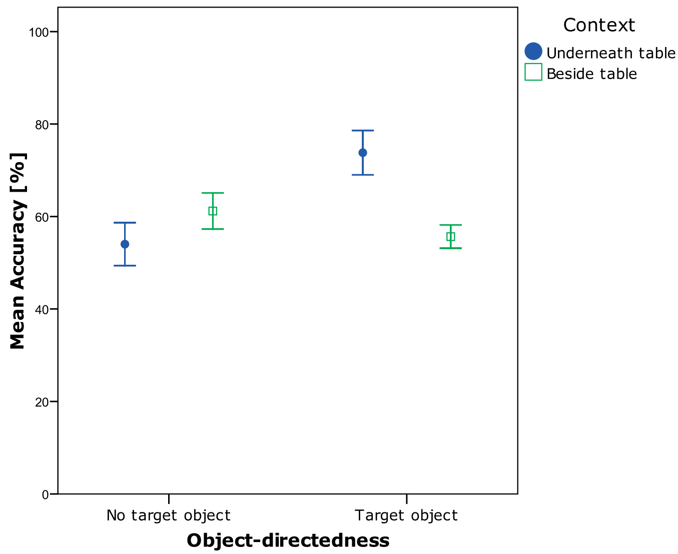

Figure 5a: Mean accuracy per condition Exp. 2B. Bars represent 95% confidence intervals of SE.

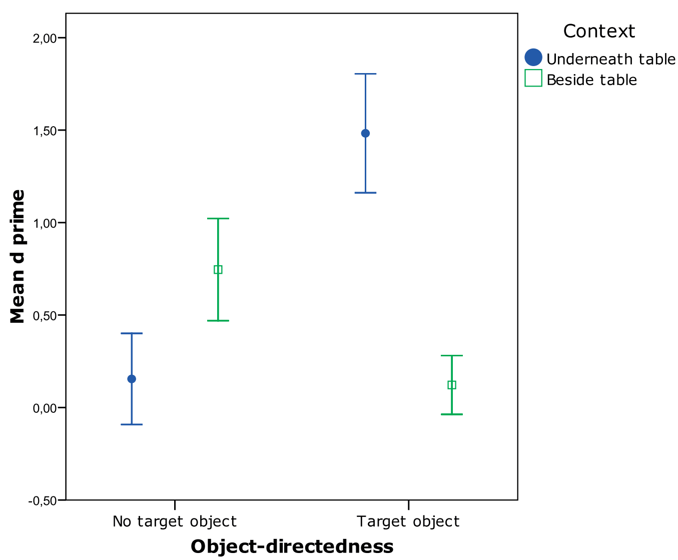

Figure 5b: Mean *d*' per condition Exp. 2B. Bars represent 95% confidence intervals of SE.

comparing the four separate conditions. The *d*'s were highest in the condition where crawling took place underneath the table towards a target object (M = 1.49), compared to the three other conditions [*t*'s(22) at least equaled 4.2 with all *p*'s < 0.001]. Comparable to the accuracy of results, the Beside table with Target object condition yielded slightly higher *d*'s (M = 0.75) than the other two remaining conditions ($M_{Underneath\_table\_x\_No\_target}$ = 0.15 and $M_{Beside\_table\_x\_Target\_object}$ = 0.12; comparisons between the Beside table × Target object condition and the other two: *t*'s at least equaled 4.4, *p*'s < 0.001). This effect disappeared when excluding the trials of one specific actor. The main and interaction effects then remained significant. The *d*'s of the Beside table with No target condition were then no longer systematically higher than the two remaining conditions [comparison with the condition Beside table with Target object: $t(22) = 2.3$, $p = 0.03$; comparison with the Underneath table with No target object condition: $t(22) = 1.13$, n.s.].

CONCLUSION

The results of Experiment 2B are in line with those of Experiment 2A, as action predictions were more accurate when the actor moved to the target object and was constrained in her action by the action context. Given that these predictions were made in the absence of visual information about the position of the target object itself, these findings suggest a crucial role of movement kinematics in action predictions. The *d*' analysis shows the same results as the accuracy data, indicating that this is not just a response bias.

Both the accuracy data and the *d*' analysis show that the trials of one of the actors yielded slightly better predictions in the condition where crawling took place beside the table with no target object compared to the Underneath table with No target and the Beside table with Target object conditions. As mentioned in the "Method" section, this actor was only included in two out of ten trials per condition as she acted in a slightly different way than the other two actors. Apparently, this difference in movements between the actors influenced the prediction accuracy of the observers.

Discussion

The current study investigated the role of visual information about target objects, situational constraints and movement kinematics for action predictions. The results of Experiment 1 show that observers are more accurate in their predictions of the next move of an actor if the action is object-directed and constrained by the situational context. Experiment 2A and 2B show that these predictions are based on the movement kinematics of the actor. Thus, people act in a more predictable manner if they are moving towards a target object and are constrained by their physical environment. This goal-directedness which resides in the movements of the actor can be effectively detected and used for predictions by the observers.

The present study was the first to test how action prediction is affected by the combination of target object information, situational constraints and movement kinematics. So far, theoretical and computational studies on action prediction suggest that action predictions are based on information about target objects and situational constraints (Gergely & Csibra, 2003; Baker et al., 2009). In Experiment 1, we replicated these findings, and the results clearly show that action prediction accuracy is highest when the action includes a target object and a situational constraint. However, from Experiment 1, it was unclear what the contribution of the actor's kinematics was to these predictions. Previous work on action observation suggests that action representations are hierarchically organized (Grafton & Hamilton 2007), such that goals are more important than means. Making the kinematics incongruent with the target of the action, as in Experiment 2A, might therefore have led to a similar pattern of action prediction accuracies as in Experiment 1. Yet, the data of Experiment 2A show the reversed pattern of results, indicating a crucial role for movement kinematics in action prediction. The results of Experiment 2B confirm this, as the absence of visual information about the target object still led participants to be more accurate in their predictions of the constrained object-directed actions compared to the other actions. In line with our results, recent empirical work indicates that movement kinematics may affect action predictions (Sartori et al., 2011; Graf et al., 2007; Stadler et al., 2012).

Although typically mentioned in the literature on action perception, the importance of movement kinematics for predicting the actions observed is undervalued. That is, it is often emphasized that actions with similar kinematics can have different goals (Kilner et al., 2007; Jacob & Jeannerod, 2005), and vice versa, similar goals can be achieved with different kinematics. Furthermore, actions with different kinematics but the same goal lead to similar activity in specific mirror neurons in monkeys (Fogassi et al., 2005), which also seems to hold for MNS activity in humans (Gazzola, Rizzolatti, Wicker, & Keysers, 2007). In addition, in behavioral studies, action goals appear to dominate the means to achieve the goal. For instance, imitation studies show that goals are imitated while means are mostly neglected (Bekkering et al., 2000; Wohlschläger & Bekkering, 2002). In reaction time studies, goal-objects evoke stronger interference effects than, for instance, means (van Elk et al., 2008a) or spatial information (Bach et al., 2005). Goals seem to be the leading factor in the action hierarchy, whereas movement kinematics are the lowest level in this hierarchy (Grafton & Hamilton, 2007; Hamilton & Grafton, 2007).

However, there are indications that movement kinematics are processed and used by observers. For instance, kinematics of observed actions have been shown to affect automatic imitation, even when the stimulus material is very abstract, such as consisting of a single dot (Bisio, Stucchi, Jacono, Fadiga, & Pozzo, 2010). Furthermore, movement kinematics can form the basis of action predictions, as illustrated by the current study. In a similar vein, other studies have reported that subtle changes in the kinematics of an observed action can be used to predict action targets (Neal & Kilner, 2010). Already in infancy, movement kinematics such as the grip aperture of the actor can form the basis for expectations about which the target object will be grasped (Daum, Vuori, Prinz, & Aschersleben, 2009). Likewise, infants can predict which target will be used based on how a multiple purpose tool is handled (Paulus, Hunnius, & Bekkering, 2011b). This means that the movements of the actor reveal that what the target object will be, before this target has been reached. Another example is that observers can predict whether a basketball shot will be in or out, based on the first few moments of the action (Aglioti, Cesari, Romani, & Urgesi, 2008). Interestingly, professional basketball players need fewer frames of the same video stimuli to come to an accurate prediction of the outcome and are more accurate than novice players. With experience, people can thus become more sensitive to the subtle differences in the movement patterns.

Taking together our results and the previous findings, the importance of movement kinematics and its role in action prediction becomes somewhat clearer. There are many situations in which the goal of an observed actor is unambiguous. In these cases, kinematics might safely be neglected. However, if the scene shows multiple goal objects or locations, movement characteristics can serve as a cue for predicting what the goal will be. This might for instance be the case when predictions are made about which object a multiple purpose tool will be applied to (Paulus et al. 2011b). Secondly, if we compare actions with similar end locations, but in one case in which a goal will be reached, and in the other case not, kinematics can also play a role in predictions. This holds for instance in a situation in which observers have to judge whether a shot at the goal is in or out (Aglioti et al., 2008), and also for our study in which the one action is object-directed and the other is not.

The stimuli of one actor produced slightly higher prediction accuracy scores than the others in one of the conditions of Experiment 2B. This suggests that there are at least some individual differences in the predictability of actions. This small difference in accuracy is related to one of the actors, and it only emerged in Experiment 2B, while the observed movements were exactly the same as in Experiment 1 and 2A. Apparently, the occlusion of the target object led the participants to direct more attention to the actual movements. This strengthens our case that the obtained results are grounded in the movements of the actors.

The results of the current study show that participants may rely on movement kinematics of an actor when making predictions about the path of the actor. To what extend these results can be generalized to other situations remains to be studied. The actions were observed from a third-person perspective, possibly making it more difficult for observers to predict how they themselves would act in that situation. Studies on MNS activity are still inconclusive about whether first person perspectives give rise to stronger motor involvement or not (Alaerts, Heremans, Swinnen, & Wenderoth, 2009; Keysers et al. 2004; Schaefer, Xu, Flor, & Cohen, 2009). To what extent people vary in the goal-directedness of their movements needs also to be studied more carefully.

A question related to this is: what movement cues do observers use for action predictions? What defines the goal-directedness in the movements of actors? There are several parameters known from action production studies which might affect the predictability of the observed actions. First of all, when approaching an obstacle, velocity is normally reduced and step width is increased already several steps before arriving at the obstacle (Vallis & McFadyen, 2003). In our study, the table functioned as an obstacle in the conditions in which the actor crawled underneath the table. Consequently, her deceleration before switching to crawling might have been stronger when confronted with the table. Second, studies on walking behavior show that larger steps combined with higher speed lead to less predictable steps (Jordan, Challis, & Newell, 2007). Step size and speed may therefore function as a parameter for predictions of observed actions. Furthermore, actions with a wider range of end locations take less time to complete than actions which are tightly constrained (Fitts, 1954), and action perception has been shown to be sensitive to this phenomenon (Grosjean, Shiffrar, & Knoblich, 2007). In the object-directed conditions of our study, the end location was more strongly bound in space than the not-objected directed conditions, which may have influenced the movements of the actors. Other parameters which may influence the predictability of observed actions are head orientation, head movements and arm movements. Pelz, Hayhoe, & Loeber (2001), for instance, show that in a naturalistic task, the pattern of head, eye and hand movements depends on the task context. To what extent action prediction is influenced by all of these movement parameters is still unknown. More experimental research is needed in which each of these factors is carefully manipulated to unravel that which type of movement cues are used in the prediction of observed actions.

In conclusion, our results show that people predict actions based on target objects and situational constraints. Predictions of ongoing actions are more accurate and sensitive if the observed action is constrained by the context and object-directed. For their predictions, observers use subtle movement cues of the observed actor, rather than direct visual information about target objects and context. The action context and target objects thus enhance predictions of an observed ongoing action, through the movement kinematics of the actor.

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Chapter 4

Prediction of Efficient and Inefficient Human Actions in Infants and Adults

Abstract

When performing actions, the motor system is thought to select movements that are the most efficient out of all possible movements to attain a planned goal. Both motor simulation theories and rationality theory suggest that adults are capable of predicting the goal when they observe an efficient action. Motor simulation theories, but not rationality theory, assume that own action experience is a prerequisite for action prediction. The current study investigated whether action efficiency enables observers to better predict action targets, .i.e., anticipate the target object of an observed action, and more crucially, whether action experience is necessary for these efficiency-based predictions. The gaze of 8- and 23-month-old infants and adults was tracked while looking at efficient and inefficient actions. The stimulus videos displayed an actor who walked first, then crawled, subsequently stood up again, and reached for and grasped a ball at shoulder-height. A part of the ceiling in the action scene was either lowered or at normal height. In the lowered ceiling situation, crawling was necessary and therefore an efficient means to get to the ball. In the high ceiling situation, crawling was considered an inefficient means as walking would have been faster. The results showed that in all age groups, participants looked equally often at the target ball compared to a distractor target prior to goal attainment in the efficient and inefficient action condition. In conclusion, no evidence was found supporting the idea that observers use principles of efficiency to predict the target of an observed action.

Keywords: Action perception; Infancy; Rationality; Context

Based on: Stapel, J.C., Hunnius, S., & Bekkering, H. (in prep.). Prediction of efficient and inefficient human actions in infants and adults.

Introduction

A mutual understanding of each other's actions is an important building block for social interaction (Carpendale & Lewis, 2004; Gallese, Keysers, & Rizzolatti, 2004). Understanding and predicting others' actions requires not only that the action itself is processed, but also the situation in which the action is embedded. In the well-known thought experiment concerning Dr. Jekyll and Mr. Hyde, the interpretation and the expected outcome of an observed action with a scalpel (Jacob & Jeannerod, 2005) might flip from "this is to cure" to "this is to hurt", depending on whether the action is conducted in an operating theatre or elsewhere (Kilner et al., 2007). This study examines whether infants and adults take the situation into account when predicting others' actions and whether own experiences with similar situations contribute to processing the situational constraints of an action.

The situation in which an action is embedded might shape predictions and expectations about the action even prior to action onset (Kilner et al., 2007; Ansuini, Cavallo, Bertone, & Becchio, 2014 Gergely, & Csibra, 2003). According to motor simulation accounts (Wilson & Knoblich, 2005; Wolpert et al., 2003), predictions of observed actions can be made by simulating the observed action in one's own motor system. In action execution, the motor system selects those movements that are the most efficient movements to accomplish a planned goal (Nelson, 1983). Observers may therefore expect others to act efficiently. A similar hypothesis can be derived from rationality theory (Gergely and Csibra, 2003). That is, adults and also infants expect agents to act efficiently and to only make detours when confronted with obstacles. Consequently, the exact same action path, moving with a detour towards a target location, can be regarded as efficient in the presence of a situational constraint or as inefficient in the absence of a constraint that would justify the detour. Most studies investigating observers' expectations of efficient and inefficient actions early in life have used infants' looking time as dependent variable (e.g., Csibra, 2008; Kamewari, Kato, Kanda, Ishiguro, & Hiraki, 2005). However, looking behavior in response to a test trial not necessarily signals whether or not predictions were made during observation of the action (Paulus et al., 2011c; Hunnius & Bekkering, 2014). Moreover, many studies on action efficiency have used relatively abstract, non-human agents (e.g., Bíró, 2013; Csibra, 2008; Gergely et al., 1995). To what extent and from what age situational constraints affect the prediction of observed *human* actions is yet unclear. Human actions are potentially more difficult to predict than actions of abstract agents as human arms and legs move in various directions with varying speed during locomotion (Full & Koditschek, 1999; Kay, 1988), making it computationally complex to derive the action path from the actor's movements (Bregler & Malik, 1998).

There are several developmental views on how infants might come to use situational constraints to judge whether an action is an efficient or an efficient means to reach an action goal. Following rationality theory, infants might apply the efficiency rule already by 6 months of age, independently of experience (Gergely, & Csibra, 2003). Alternatively, predictions may be based on motor simulation and in that case infants might use their (action) experience with comparable situations to judge whether an action is efficient or inefficient given the situational constraints (Hunnius & Bekkering, 2014).

To shed more light on the development of action prediction based on situational constraints, an eye-tracking experiment was conducted with participants from different age groups, who were presented with efficient and inefficient actions. The actor in the stimulus videos first walked before she started to crawl and then got up again to reach and grasp for a ball. The crawling was either an efficient means to get to the ball or an inefficient means, depending on the height of a part of the ceiling in the room where the action was situated. When the ceiling was low, crawling was the only way to get to the target, whereas walking would have been more efficient when the ceiling was high. Eight-month-old infants, 23-month-old toddlers, and a group of adults participated in the experiment. If the development of action prediction based on situational constraint is driven by own action experience, then the 23-month-olds and adults, but not the 8-month-olds should process the actions differently. That is, for 8-month-olds, who are capable of crawling but not yet of walking, crawling is an efficient means to get from A to B, regardless of the situation. For 23-month-olds, who are capable of crawling but who also have extended walking experience, walking is the most efficient means to get from A to B, if the situation permits walking. Moreover, additional evidence for the role of action experience would be a significant relationship between the individual walking experience and the extent to which individuals predict the efficient and not the inefficient action. To that end, a parental questionnaire was used to assess the individual walking experience of the toddlers. Rationality theory, on the other hand, predicts that all three age groups would be capable of predicting the efficient action, and no relationship should be observed with walking experience.

Method

Participants

A group of 8-month-old infants (N = 25, Mean age = 8.2 months, SD = 0.3 months, 12 females), a group of 23-month-old toddlers (N = 24, Mean age = 23.2 months, SD = 0.3 months, 14 females), and a group of adults (N = 17, Mean age = 25 years, SD = 4 years, 12 females) participated in the study. The infants and toddlers were recruited from the database of the Baby Research Center Nijmegen, which contains the names and addresses of parents who indicated to be willing to partake in infant research. Prescreening was applied prior to the test sessions of infants and toddlers to select 8-month-old infants capable of (belly-) crawling but not yet capable of cruising or walking independently. Despite this prescreening procedure, four 8-month-olds could not be included in the final sample as they were capable of walking already at test (N = 2), or not yet capable of (belly-) crawling at the day of testing. The adults signed up through a participant portal for persons willing to participate in experiments of the Radboud University Nijmegen or via an experimenter who advertised the study. Data of one other adult were collected but not included in the data analyses, due to an insufficient amount of valid trials (2 out of 48). Written informed consent was obtained from the parents and the participating adults prior to the study. As a thank you for their participation, the participating children and their parents received an infant book or 10 Euros, and the participating adults received a gift voucher of 5 Euros or credit points.

Walking experience of the 23-month-old toddlers

The group of 23-month-old toddlers had on average 38 weeks experience with walking independently when they entered the lab. There was substantial variability in the toddlers' walking experience, which ranged between 16 and 61 weeks (SD = 11 weeks).

Stimuli

The participants were presented with stimulus videos showing an avatar which was animated based on human movement recordings. A previous study using comparable movements showed that a transition from walking to crawling is more predictable if the crawling is constrained (for instance because the crawling takes place under a table) compared to if it is unconstrained (Stapel, Hunnius, & Bekkering, 2012). For the current study, the purpose was to manipulate the action constraints, while keeping the movements of the actor identical across conditions. Therefore, movements of an actor were recorded with an MVN Biomech motion tracking system (XSens, Enschede, the Netherlands) consisting of 17 inertial sensors tracking the movements of the actor at 120 Hz. The actor started moving from an upright position, walked a step forward, turned to crawling, crawled a few cycles and stood up again to reach for and grasp a ball located at shoulder height. The actor's movements were recorded in a constrained and an unconstrained situation, as the crawling took place underneath a table frame or in a space without the table frame. Subsequently, the recorded movements were applied to an avatar using MotionBuilder (Autodesk, San Rafael, USA). The avatar was positioned in a 3D virtual environment constructed in 3DS Max (Autodesk, San Rafael, USA). Stimulus videos containing both the virtual environment and the avatar were rendered in Vizard 3.0 (World Viz, Santa Barbara, USA) and finalized in VirtualDub 1.6.19 (Avery Lee). Three constrained and three unconstrained movement recordings were used, leading to 6 different movements.

Three types of video stimuli were presented during the experiment, all of them 720 pixels high and 1280 pixels wide. The first stimulus video, based on recorded movements as well, displayed actor walking with a ball in her hands, showing the ball to the observer. This illustrated that the actor was capable of walking. The ball depicted in the first stimulus was the target of all actions shown subsequently. After the first stimulus, 24 (in case of the infant and toddler participants) or 48 (adults) trials were presented in random order. In the stimuli, the actor could be observed making the recorded movements, with added still frames at the start (actor standing for 0.5 sec) and at the end of the action (actor standing holding the ball for 1 sec, see Fig.1). Stimulus duration ranged between 10.6 and 11.7 seconds (M = 11.3 sec). The observed crawling took place in a little house in which the ceiling was either at normal height so that it permitted walking or lowered (see Fig. 2A and 2B). For both stimulus backgrounds, all 6 different movements were used, leading to identical movements across conditions and 12 unique stimulus videos. Not only the target ball, but also a second ball was included in the scene as a distractor stimulus. We examined whether participants predicted the actor to grasp the target ball and thus compared the frequency of anticipatory looks to both balls across conditions and age groups. The non-target ball was located at the same side of the stimulus as the target ball, but on the floor, whereas the target ball was positioned at shoulder-height. Consequently, crawling in the high-ceiling condition should bias goal-inferences to the low ball on the floor (i.e. the non-

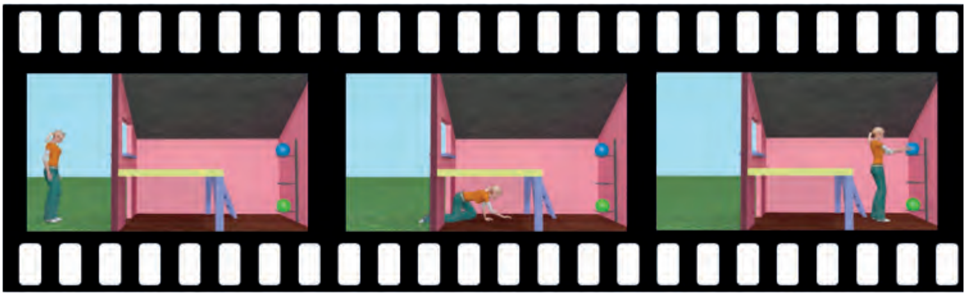

Figure 1: Example frames taken from one of the stimulus videos.

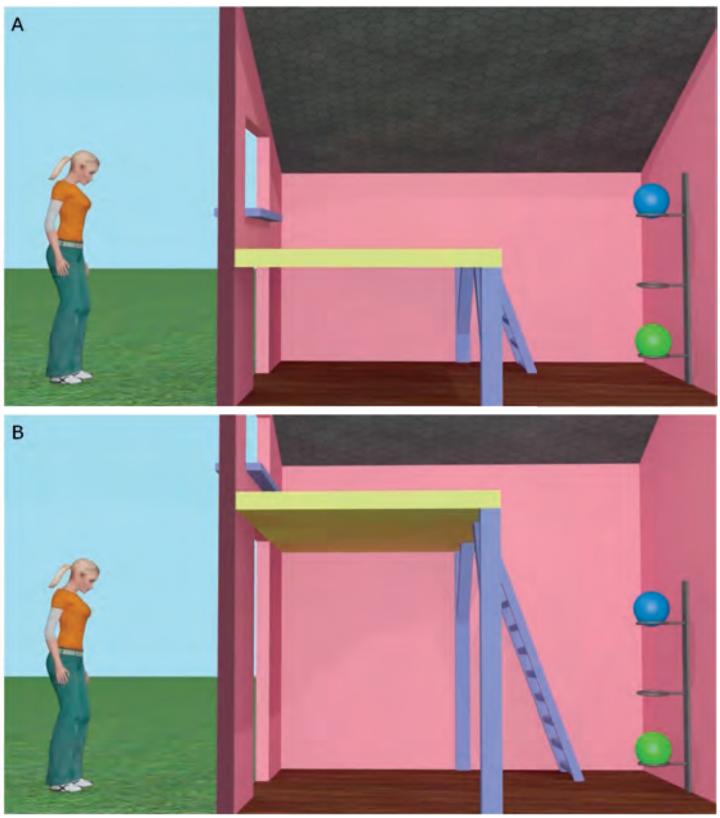

Figure 2: First frame of an Efficient (A) and of an Inefficient (B) action stimulus.

target ball), whereas crawling in the low-ceiling condition was not informative about whether the actor would go for the high or low ball. The color of the target ball (either green or blue) was counterbalanced between participants. The non-target ball was blue when the target ball was green and green when the target ball was blue.

Procedure

Upon arrival in the lab, participants were seated in front of the computer monitor of a Tobii 1750 eye-tracker (Tobii Technologies, Danderyd, Sweden). Infants were placed in a car seat on their caregiver's lap. Toddlers who were better able to sit in a stable and upright position were seated directly on their caregiver's lap, and adult participants were seated on a height-adjustable office chair. All participants first underwent a calibration procedure in which a contracting and expanding circle was presented on the screen on 9 different locations after each other, forming a 3-by-3 grid. The visual stimulus was accompanied by a sound to attract attention to the screen. The calibration was considered successful if data was gathered for 7 or more grid locations. Immediately after the calibration procedure, the experiment started and video stimuli were displayed on the eye-tracker screen (resolution: 1024 by 1280) while the participants' gaze was registered. To maintain the attention to the screen, the experimental stimuli were interleaved with attractive audiovisual clips (7 for the children, 2 for the adults). After the experiment, parents and adult participants were debriefed, thanked, and everyone received a small gift for participation.

Analyses

For the analyses, equally-sized square-shaped areas of interest (AoIs, 145 by 145 px) were defined around the target and non-target ball (see Fig. 3). Furthermore, a stimulus AoI was defined containing the complete display (720 by 1280 px). Per participant and per condition, we counted the number of trials in which the participant fixated at least once on the stimulus display. The infant and toddler participants attended to at least 10 trials per condition, the adult participants watched all trials. Per participant and condition, trials were counted in which the participant looked at either of the ball AoIs while the actor was crawling. The crawling period was the chosen period of interest, as during that period it was ambiguous which ball would be the target of the action. The number of trials with anticipatory fixations to the target and non-target ball was divided by the number

Figure 3: Areas of interest were defined around the target ball (blue AoI) and the non-target ball (yellow AoI).

of watched trials, and expressed as percentage per condition and per participant. A mixed repeated measures ANOVA was used to investigate whether age and the efficiency of the observed action affected the percentage of target and non-target anticipations. If all age groups would display more frequent visual anticipations to the target in the efficient condition (or less frequent anticipations to the non-target), then this would serve as support for rationality theory. If only the older age groups would display such an effect, then motor simulation might underlie the predictions found. In that case, it would be meaningful to conduct a follow-up analysis to investigate whether individual walking experience of the 23-month-olds is correlated with the ability to predict the efficient actions under study.

Results

Anticipatory fixations

The repeated measures ANOVA with ball (target, non-target) and action efficiency (efficient, inefficient) as within-subjects factors and age group (8-month-olds, 23-month-olds, adults) as between-subjects factor was conducted on the percentage of anticipatory looks to either of the balls. The analysis yielded a significant interaction effect of age and the type of ball ($F(2,63) = 5.65$, $p = 0.006$). Post-hoc paired-samples t-tests revealed that the adults and the 8-month-old infants did not differ in their frequency of anticipatory looks to the target (adults: M = 23%, SD = 20; 8-month-olds: M = 8%, SD = 10) compared to the non-target ball (adults: M = 17%, SD = 8; $t(16) = 1.25$, $p = 0.228$; 8-month-olds: M = 12%; SD = 8, $t(24) = -0.61$, $p = 0.550$, see Fig. 4), whereas the 23-month-old toddlers displayed more frequent anticipatory looks to the non-target ($M_{non\text{-}target}$ = 28%, SD = 16) than to the target ball (M_{target} = 17%, SD = 10; $t(23) = -3.14$, $p = 0.005$). Furthermore, a significant interaction between the type of ball and action efficiency was found ($F(1,63) = 7.33$, $p = 0.009$). Post-hoc paired-samples t-tests showed that there were no significant differences found between the efficient and inefficient action in the frequency of anticipatory looks to the target ball ($M_{efficient}$ = 15%, $SD_{efficient}$ = 16; $M_{inefficient}$ = 17%, $SD_{inefficient}$ = 16; $t(65) = 0.76$, $p = 0.451$, see Fig. 5), but participants looked more frequently to the non-target ball for the efficient (M = 20%, SD = 19) compared to the inefficient action (M = 15%, SD = 15; $t(65) = -2.20$, $p = 0.032$). The difference between the frequency of anticipatory looks to the non-target in the efficient and the inefficient condition was not found to be significant in the separate age groups ($ts < 1.5$, $ps > 0.15$) , indicating that the effect only emerges when aggregating the data of the 3 age groups (see also Fig.6).

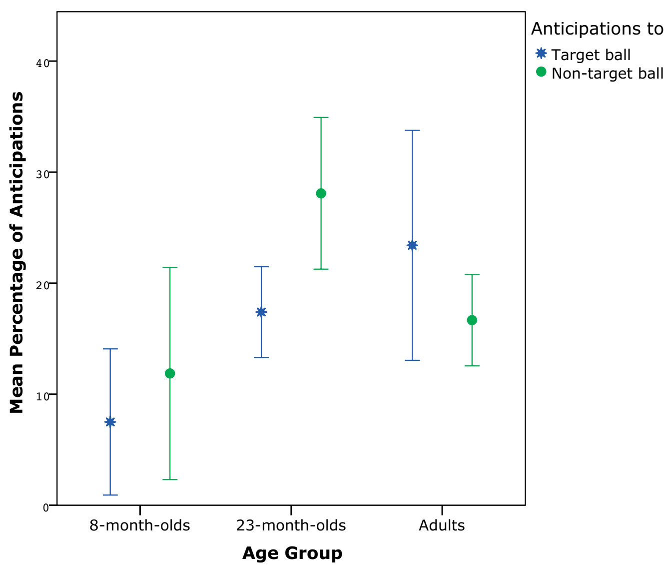

Figure 4: Mean percentage of trials in which participants fixated at the target or non-target ball while the actor was crawling, split by age group and the type of ball (target versus non-target). Error bars represent 95% confidence intervals around the means.

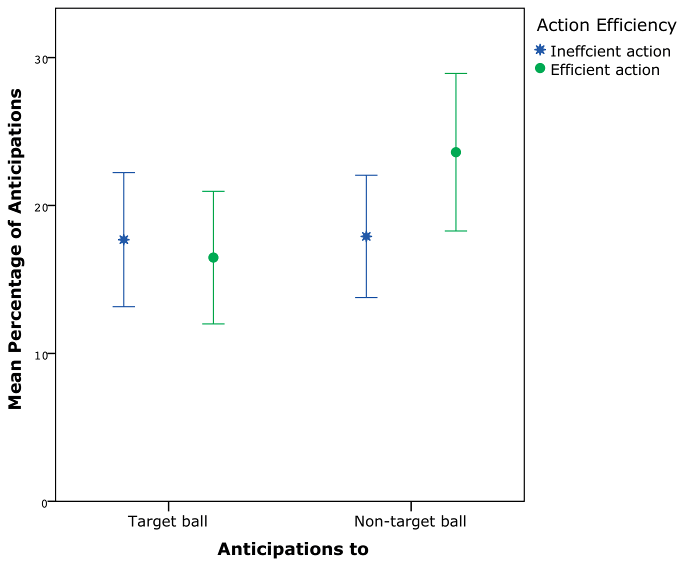

Figure 5: Mean percentage of trials in which participants fixated at the target or non-target ball while the actor was crawling, split by action efficiency and the type of ball (target versus non-target). Error bars represent 95% confidence intervals around the means.

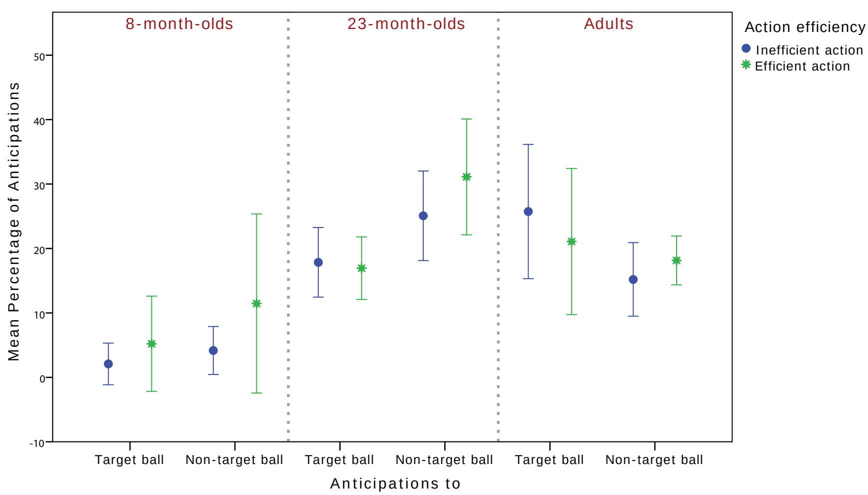

Figure 6: Mean percentage of trials in which participants fixated at the target or non-target ball while the actor was crawling, split by age group, action efficiency and the type of ball (target versus non-target). Error bars represent 95% confidence intervals around the means.

One of the difficulties of experimental action prediction research is that participants may learn to predict the observed actions through the repeated presentation of the stimuli (Henrichs, Elsner, Elsner, & Gredebäck, 2012; Henrichs, Elsner, Elsner, Wilkinson, & Gredebäck, 2014). Learning within the experiment might diminish conditional differences that would otherwise be found. For that reason, a post-hoc follow-up analysis was carried out to investigate whether target predictions depended on action efficiency at the start of the experiment. Percentages of the first two trials per condition were analyzed with the same type of ANOVA as used to analyze the effect of action efficiency across all trials. The results showed (amongst others) a significant three-way interaction between age, type of ball, and action efficiency ($F(2,63) = 3.16$, $p = 0.049$). Repeated measures ANOVAs on the separate age groups were used to gain insight into the three-way interaction. These ANOVAs revealed a marginally significant interaction between type of ball and action efficiency in the group of 23-month-olds ($F(1,23) = 4.06$, $p = 0.056$), and a similar, significant interaction in the adult group ($F(1,16) = 7.17$, $p = 0.017$), but not in the 8-month-olds($F(1,24) = 0.24$, $p = 0.627$). A paired-samples t-test indicated that the target ball was more frequently anticipated in the inefficient (M = 33%, SD = 32) compared to the efficient condition (M = 15%, SD = 28, $t(23) = 2.58$, $p = 0.017$) by the 23-month-olds. The same contrast in the adult sample did not reach significance ($M_{efficient} = 35\%$, $SD_{efficient} = 34$; $M_{inefficient} = 47\%$, $SD_{inefficient} = 41$; $t(16) = 1.29$, $p = 0.216$). In both the 23-month-old group and the adult group, the difference between visual anticipations to the non-target ball in the efficient (23-mo.: M = 46%, SD = 36; adults: M = 47%, SD = 37) compared to the inefficient condition (23-mo: M = 40%, SD = 42; adults: M = 26%, SD = 40) was found to be not significant (23-mo.: $t(23) = -0.59$, $p = 0.560$; adults: $t(16) = -1.69$, $p = 0.110$). More details of these analyses can be found in the supplementary materials.

Discussion

The current study aimed to investigate whether predictions of observed actions depend on situational constraints that have an impact on the efficiency of the observed action. In addition, the developmental timeline and the role of motor experience for predictions based on action constraints were studied. No evidence was found for the notion that the action targets of efficient actions are more predictable than the targets of inefficient actions as no difference was found in the frequency of anticipatory looks to the target between the efficient and the inefficient action condition. These results seem somewhat incompatible with rule-based inferential action processing as laid out in rationality theory (Gergely & Csibra, 2003), which predicts that infants and adults, regardless of their action experience, can predict efficient actions. Expectations derived from motor theories were also not met, as motor theories would predict that infants and adults capable of performing the observed action would also be capable of basing their predictions on action efficiency. In sum, the results are incompatible with both rationality theory and motor simulation theories, as none of the age groups was found to make efficiency-based predictions.

Action prediction, and more specifically the prediction of the target location of an observed action, was expected to be based on situational constraints and hence the efficiency of the observed action. The hypothesis that efficient actions would be more predictable than inefficient actions can be derived from multiple theoretical accounts. Rationality theory (Gergely, & Csibra, 2003) postulates that infants and adults expect others to act efficiently, and hence, observers are supposed to be capable of predicting efficient, but not inefficient actions. Motor theories (Wolpert, 1997; Nelson, 1983) and theories about motor simulation and prediction (e.g., Wolpert et al., 2003) would claim that the motor system selects the most optimal and efficient actions during action production and therefore efficiency is expected to play a role in action observation as well. More broadly, constrained actions have fewer degrees of freedom and can therefore be expected to be more predictable. Both rationality theory and motor theories would therefore predict that action constraints enable observers to better predict the outcome of the observed action.

However, the current results lend no support for the notion that actions are more predictable when they are constrained by the situation compared to when the action is unconstrained. There was no difference in anticipatory looks to the target in the efficient compared to the inefficient condition, not even in the group of adults. Participants were even more likely to look at the non-target ball during the efficient action. Potentially, participants inferred that the actor could not see the target while crawling underneath the low ceiling, and therefore did not expect the actor to go the target, but rather expected the actor to go for the ball that was in the line of sight of the actor during crawling (i.e. the non-target ball). A potential explanation for the non-significant difference between target-predictions in the efficient and the inefficient action is the multi-facetted aspect of the action. It is known from joint action research investigating multi-step actions that co-actors tend to generate predictions about and plan ahead for the first step of the co-actors actions (e.g., the reaching for an object, see Ray & Welsh, 2011), but do not immediately take the second step (e.g., subsequently placing the object at a different location, see Meyer, van der Wel & Hunnius, 2013) into account when acting jointly. Another reason might be that in normal situations, the actor's movements may form the primary source of information for action prediction (Stapel et al., 2012), and information about the action constraints is not necessary in those cases. Based on the velocity profile (Graf et al., 2007) together with curvature of the action (Flash & Hogan, 1985) observers can make predictions about the end-location of an action. If the movements are uninformative about the target of the action and predictions have to solely rely on the situation, generating action predictions might thus be more difficult. Adults have been shown to be capable of learning to predict the future course of an action path, including the path of efficient actions (Paulus et al., 2011c; Kayhan, Monroy, Gerson, Hunnius, & Bekkering, in prep.), but these predictions were only made if prior information was available. For instance, having frequently observed the same efficient action might enable adults to predict the future path of that action (Paulus et al., 2011c; Kayhan et al., in prep.).

Actions are not performed in a vacuum, but embedded in situations. In theory, action constraints can be informative for the prediction of the target of an action (Gergely & Csibra, 2003; Kilner et al., 2007). However, in the current study, no evidence was found indicating that action constraints are taken into account when predicting the target of an action. Potentially, the multi-step nature of the action used in the current study prevented observers from using the action constraints for the generation of goal-predictions, but rather enabled them to make predictions about the first next step of the action. Therefore, more research is needed to unravel whether and how action constraints are used for action prediction. Action constraints can rule out some of the many future courses an unfolding action might take. Therefore, action constraints may turn out to be a valuable source of information for action prediction, though more empirical research is needed to investigate whether constraints indeed inform the prediction of others' actions.

Acknowlegdements

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Supplementary materials

Anticipations in the first two trials

A repeated measures ANOVA was conducted to analyze the anticipation frequency during the first two trials per condition. The within-subject factors used were ball (target, non-target), and action efficiency (efficient, inefficient), and age group (8-month-olds, 23-month-olds, adults) was included as a between-subjects factor. A main effect of age was found ($F(2,63) = 10.57$, $p < 0.001$), indicating that 8-month-olds anticipated either of the balls less frequently (M = 12%, SD = 16) than 23-month-olds (M = 33%, SD = 22, $t(42.7) = -3.89$, $p < 0.001$) and adults did (M = 39%, SD = 25, $t(25.5) = -3.97$, $p = 0.001$). The adults and 23-month-old infants did not differ significantly in their anticipation frequency ($t(39) = -0.78$, $p = 0.442$).

The ANOVA furthermore yielded a significant interaction between ball and age group on the anticipation frequency ($F(2,63) = 3.33$, $p = 0.042$). Post-hoc paired-samples t-tests revealed that 8-month-olds (M_{target} = 11%, SD = 16, $M_{non\text{-}target}$ = 13%, SD = 23, $t(24) = -0.44$, $p = 0.664$) and adults (M_{target} = 41%, SD = 33, $M_{non\text{-}target}$ = 37%, SD = 29, $t(16) = 0.47$, $p = 0.645$) did not display a difference in the frequency of anticipating to the target and non-target ball, whereas 23-month-olds did ($t(23) = -3.00$, $p = 0.006$). The 23-month-olds looked more frequently at the non-target ball (M = 43%, SD = 29) than the target ball (M = 24%, SD = 24) while the action was still unfolding.

In addition, action efficiency and type of ball had a combined effect on the frequency of anticipatory looks ($F(1,63) = 7.77$, $p = 0.007$). While anticipations to the non-target ball did not differ in frequency for the efficient (M = 34%, SD = 36) and inefficient action condition (M = 26%, SD = 37%, $t(65) = -1.56$, $p = 0.124$), anticipations to the target ball did differ marginally ($t(65) = 1.80$, $p = 0.077$). More frequent target anticipations were observed in the inefficient (M = 27%, SD = 34) compared to the efficient action condition (M = 20%, SD = 29).

Lastly, action efficiency, type of ball and age group were found to have a significant three-way interaction effect on the anticipation frequency ($F(2,63) = 3.16$, $p = 0.049$). Repeated measures ANOVAs were run on the data of the three age groups separately to find which of the groups showed a significant interaction of action efficiency and ball on the frequency of anticipatory looks. This interaction was found to be (marginally) significant for the 23-month-olds ($F(1,23) = 4.06$, $p = 0.056$) and the adults ($F(1,16) = 7.17$, $p = 0.017$), but not for the 8-month-olds ($F(1,24) = 0.24$, $p = 0.627$). The 23-month-old infants anticipated more frequently to the target in the efficient compared to the inefficient condition ($t(23) = 2.58$, $p = 0.017$), whereas such conditional differences were not found for visual anticipations to the non-target ($t(23) = -0.59$, $p = 0.560$). In the adult data, no differences were found between the efficient and inefficient action condition in the frequency of anticipations to the target ball ($t(16) = 1.29$, $p = 0.22$), and the same held for anticipations to the non-target ball ($t(16) = -1.69$, $p = 0.11$). The absence of a significant difference in either of the t-tests shows that the interaction was significant only because the difference of the difference was significant. There tended to be more target anticipations in the inefficient (M = 47%, SD = 41) compared to the efficient condition (M = 35%, SD = 34), whereas there tended to be more non-target anticipations in the efficient (M = 47%, SD = 37) compared to the inefficient condition (M = 26%, SD = 40).

Chapter 5

Motor System Contribution to Action Prediction: Temporal Accuracy Depends on Motor Experience

Abstract

Predicting others' actions is essential for well-coordinated social interactions. In two experiments with an infant population, this study addresses to what extent motor experience of an observer determines prediction accuracy for others' actions. Results show that infants who were proficient crawlers but inexperienced walkers predicted crawling more accurately than walking, whereas age groups mastering both skills (i.e. toddlers and adults) were equally accurate in predicting walking and crawling. Regardless of experience, human movements were predicted more accurately by all age-groups than non-human movement control stimuli. This suggests that for predictions to be accurate, the observed act needs to be established in the motor repertoire of the observer. Through the acquisition of new motor skills, we also become better at predicting others' actions.

The findings thus stress the relevance of motor experience for social-cognitive development.

Keywords: Action prediction; Simulation; Prediction accuracy; Motor system

Based on: Stapel, J.C., Hunnius, S., Meyer, M., & Bekkering, H. (in revision). Motor system contribution to action prediction: Temporal accuracy depends on motor experience.

Introduction

Predicting others' actions is crucial for acting in a social world. For social interaction to run smoothly, accurate predictions of the precise timing of the partner's movements are necessary (Sebanz & Knoblich, 2009). According to the simulation account (Wilson & Knoblich, 2005), the motor system generates predictions of how observed actions will continue in time and space. These predictions are thought to be based on the motor program a person uses for executing the same action (Kilner et al., 2007; Prinz, 2006; Wolpert et al., 2003). Studies contrasting human and non-human movements provide a first indication that the motor system is indeed involved in the prediction of actions and their timing: Though human motion should be much harder to predict due to its complexity, empirical results show the opposite (Saunier, Papaxanthis, Vargas, & Pozzo, 2008; Stadler et al., 2012). The current study investigated whether the motor system is crucially involved in action prediction by comparing how well groups with different motor experiences can predict different actions.

Previous neuroimaging studies showed that the motor system is not only involved in action execution, but also in action observation (e.g., Candidi, Sacheli, Mega, & Aglioti, 2014; de Bruijn, Schubotz, & Ullsperger, 2007; Glenberg et al., 2010; Hari et al., 1998; Malfait et al., 2009; Rizzolatti et al., 1996a). Motor activation in adults is found to be stronger if the observer has more motor experience with this action (Calvo-Merino et al., 2005, 2006; Cross et al., 2006). The same holds for infants as shown in a study by Van Elk and colleagues (2008b). The tested 14- to 16-month-old infants, who were experienced crawlers but inexperienced walkers, displayed stronger motor activation while watching crawling compared to walking movements. Motor experience thus changes action perception. But does it also have an impact on the accuracy of for example temporal action predictions? Presumably, the internal model that predicts the sensory consequences of a motor command, also called a forward model (Wolpert et al., 2003), becomes more fine-grained through action experience. Such an experience-based forward model would then result in predictions of observed actions that become more accurate with increasing action experience.

Converging evidence suggests that the motor system plays an important role in the prediction of perceived actions. That is, the motor system is active during action prediction tasks (Fontana et al., 2012) prior to goal attainment (Umiltà et al., 2001), and sometimes even prior to action onset (Kilner et al., 2004). Motor activation is stronger when the observed action is not yet completed than when the goal is attained (Urgesi, Moro, Candidi, & Aglioti, 2006; Urgesi et al., 2010). The accumulating evidence from the neuroimaging literature, however, leaves open the question whether there is a measurable behavioral benefit of the involvement of the motor system when observing another person's action. One benefit illustrated in many recent studies is that infants more readily infer the end location of an observed action if that action is part of their motor repertoire. For instance, infants are quicker to infer the end location of a human compared to a non-human action (Cannon & Woodward, 2012; Falck-Ytter et al., 2006; Kanakogi & Itakura, 2011) and quicker to make a goal inference if they are more proficient in the action they observe (Ambrosini et al., 2013; Gredebäck & Kochukhova, 2010; Kanakogi & Itakura, 2011). Opponents of this interpretation argue that goal inference improves due to general motor maturation rather than as a result of increased active experience with the specific actions involved (Southgate, 2013). It thus still needs to be examined whether the prediction of an action benefits from experience with specifically this action and whether motor involvement supports precise temporal predictions which are needed in everyday social interactions.

To answer these questions, the current study compares the prediction accuracy of actions that are either part of the observer's motor repertoire or not. To that end, the participant groups were selected such that they had different motor capabilities because of their age. This developmental approach provides a unique opportunity to study the benefits of action experience for the prediction of observed actions in a natural training setting, namely by examining the impact of real-life experiences. Initially, testing and comparing prediction accuracy over different age groups might appear difficult, as reaction times tend to be slower and more variable in young children, making it hard to weigh their reactions against those of older age groups. However, the oculomotor system reaches adult levels of functioning early in life (Hunnius, 2007), which makes gaze location and gaze timing suitable measures to test action prediction performance across age groups (Falck-Ytter et al., 2006; Hunnius & Bekkering, 2010). When predicting the trajectory of objects reappearing from behind an occluder, even infants have been shown to take into account complex velocity profiles of moving objects (e.g., circular movement by 9 months of age, Gredebäck, von Hofsten, & Boudreau, 2002). In a similar fashion, gaze timing to a post-occluder area was used as a measure of action prediction accuracy in the current study. All participants observed videos of an actor or object moving from one side of the scene to the other. The actor briefly disappeared behind an occluder and then reappeared on the other side (see Fig. 1). The participants' ability to accurately predict when the actor or object would reappear was investigated. Besides prediction accuracy, the stability of the predictions was measured, which also provides information about the underlying prediction process: whereas high variability in prediction accuracy might reflect guessing, little variability likely stems from a well-established process (Zanone & Kelso, 1997).

To investigate whether differences found in action prediction accuracy between age groups are not due to general (motor) maturation, but related to motor experience with the specific actions observed, different actions were used. Experiment 1 served as a proof of concept, comparing 14-month-old infants (experienced crawlers, inexperienced walkers) with 30-month-old toddlers and adults (experienced in both walking and crawling). The infant group was expected to be more accurate and stable in predicting crawling compared to walking, whereas the other age groups were to be equally stable and accurate in predicting both actions. In Experiment 2, 18- to 20-month-old toddlers were investigated to test whether relatively little walking experience would be sufficient to accurately predict walking.

In both experiments, a third condition was included which displayed an object moving through the scene. This allowed for a comparison between predictions of movements that can be generated by the motor system and movements that are probably predicted using other brain areas, such as Medial Superior Temporal area (MST) and Middle Temporal area (MT, Newsome, Wurtz, Dursteler, & Mikami, 1985; Tanaka & Saito, 1989). These areas respond to non-biological movements in a visual scene in macaque monkeys, and especially MST is responsive to the direction of movement in humans as well (Smith, Wall, Williams, & Singh, 2006). In line with previous research (Saunier et al., 2008; Stadler et al., 2012), predictions of human movements were expected to be more accurate and stable than predictions of the non-human movements.

Experiment 1

METHOD

Subjects

Sixteen right-handed adults (11 females, mean age = 22.8 years, SD = 3.6), seventeen infants (10 females, mean age = 14.0 months, SD = 0.26), and twenty-three toddlers (6 females, mean age = 29.9 months, SD = 0.33) were tested. Two additional infants and two additional toddlers were tested but data were not included in the analyses due to insufficient calibration of the eye-tracker. All children were recruited via the database of the Baby Research Center Nijmegen, which consists of parents who signed up for participation in child research. The adults were recruited via the university's participant database. Participants in the adult sample and parents of the child participants gave written informed consent for participation (either their own or their child's) in the study.

Procedure

All participants were presented with the same set of stimuli on a Tobii 1750 eye-tracker (Tobii Technology, Stockholm, Sweden). First, a calibration procedure was administered, during which participants viewed contracting and expanding circles placed on a 3 by 3 (children) or 4 by 4 grid (adults). Data was included in the analyses if sufficient information for minimally 7 (children) or 14 (adults) calibration points was available. After calibration, 48 (children) or 96 (adults) stimulus repetitions were presented in random order, interleaved with brief audiovisual clips to maintain attention to the screen.

Materials

The stimulus material consisted of short movies displaying either an object or an infant actor moving from left to right or right to left in the scene (8 different movies per condition, duration: 73-112 frames, 25 frames per second). The six different infant actors were filmed while either walking or crawling towards their parent who was not visible in the stimulus. Part of the stimulus was occluded by a black rectangle (290 x 396 px), so that the actor's or object's movements were hidden from view for 280 to 720 ms during each stimulus presentation (see Fig. 1). The occluder was located 30 pixels from the side of the stimulus display where the movements would end, leaving open a small area of the scene where the actor or

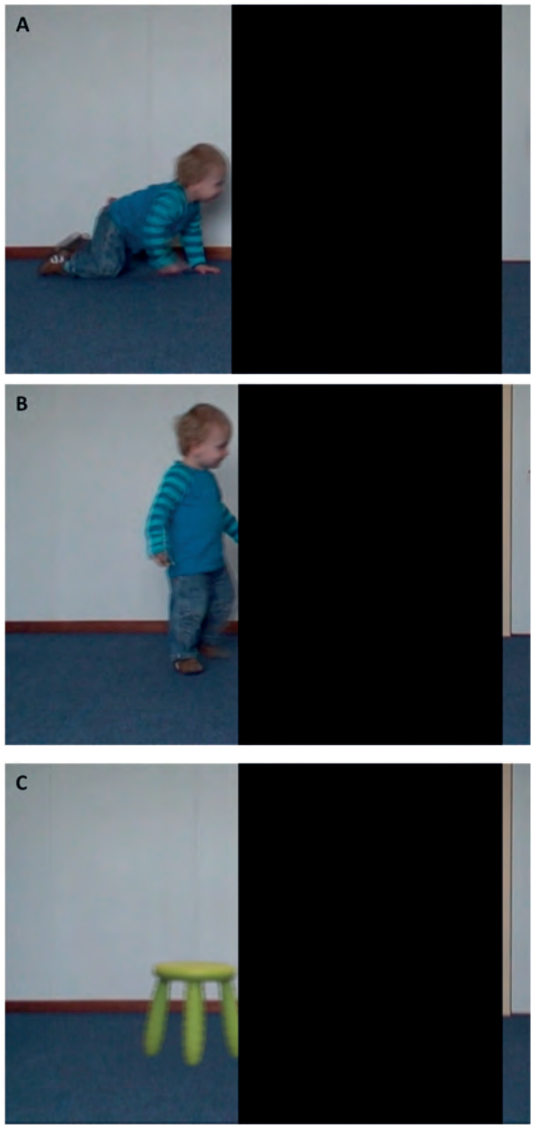

Figure 1: Example frames from the three stimulus conditions, A) infant crawling, B) infant walking, and C) moving object.

object would reappear after occlusion. Occlusion duration was varied to ensure that predictions could not be based on fixed timing after stimulus onset. Variation in occlusion duration was achieved by selecting videos of actors who differed in velocity. The different durations were matched across conditions. The time from stimulus onset to full occlusion of the actor or object was fixed (55 frames). The stimulus videos containing the object were created with Adobe Premiere (Adobe, San Jose, USA). Different objects were used to match the variety in actors. The objects were first cut out (using Adobe Illustrator) from a frame of a video recorded in the same room as the infant actors to ensure similar lighting conditions. Then, the objects were moved through the background scenes with constant velocity using Adobe Premiere. Occlusion durations were matched with the infant actor stimuli.

A parental questionnaire was put together with questions about the children's walking experience. Questions concerned the start date of supported and independent walking and the certainty with which parents could recall these dates. Many parents reported having noted down the developmental milestones of their infant in a diary. The questionnaire was filled in only by the infants' parents to assess whether they indeed had little walking experience.

RESULTS

The area of the scene where the actor or object would reappear was used as an Area of Interest (AoI) in the eye movement analysis. Data from the first 200 ms of every stimulus presentation was excluded, because gaze may still have lingered at a location determined by the previous stimulus movie. The stimulus movies continued for minimally 9 frames (360 ms) after reappearance of the actor. To allow comparisons between conditions, fixations initiated after 360 ms were discarded. Fixations to the AoI throughout the stimulus presentation were identified, and fixations closest in time to the moment of reappearance were selected. Fixations to the post-occluder area are expected to be aligned in time with the reappearance of the actor or object (Bennett & Barnes, 2006). Hence, the difference in the onset of fixation to the AoI and the actual reappearance of the actor or object was taken as an index of prediction accuracy. Furthermore, per participant, the standard deviation of the timing of the fixations was calculated per condition and used as a measure for prediction stability.

Repeated measures ANOVAs were conducted with Type of movement (crawling, walking, object) as within-subjects factor and Age group (infants, toddlers, adults) as between-subjects factor. Overall prediction accuracy ($F(1.7, 89.3) = 33.8$, $p < 0.001$, $\eta p = 0.39$)[2] and stability ($F(2,104) = 19.1$, $p < 0.001$, $\eta p = 0.27$) were higher for the human actions compared to the object movement, as indicated by a main effect of Movement type. Effects as described were further examined using paired-samples t-tests (Movement type and Age by Movement type interaction) and independent samples t-tests (Age). Detailed outcomes of these tests can be found in Tables 1, 2 and 3. Predictions of crawling movements tended to be more stable than of walking movements ($t(54) = -1.91$, $p = 0.06$), and this effect seems to be driven by infant group (see Fig.3). A comparison of the age groups ($F(2,52) = 25.28$, $p < 0.001$, $\eta p = 0.49$) shows that infants were least stable in their predictions, followed by the toddlers. Infants were also less accurate in their predictions compared to adults and toddlers ($F(2,52) = 9.24$, $p < 0.001$, $\eta p = 0.26$).

Our analyses focused on whether the age groups differed in prediction performance for the three movements and revealed significant interaction effects between Age and Movement type for both prediction accuracy ($F(3.4, 89.3) = 6.31$, $p < 0.001$, $\eta p = 0.20$) and prediction stability ($F(4,104) = 6.36$, $p < 0.001$, $\eta p = 0.20$). Infants were less accurate ($t(15) = 3.27$, $p < 0.01$) and less stable ($t(15) = -4.66$, $p < 0.001$) in their predictions of walking compared to crawling actions, whereas adults and toddlers displayed equally stable and accurate predictions for both walking and crawling (see Table 1 and 2). Predictions for human movements were more accurate and stable than for the object movements in all age groups (see Table 1 and 2).

2 In cases in which sphericity could be not assumed as indicated by a significant outcome of Mauchly's test of Sphericity, Huynh-Feldt corrected ANOVA results are reported.

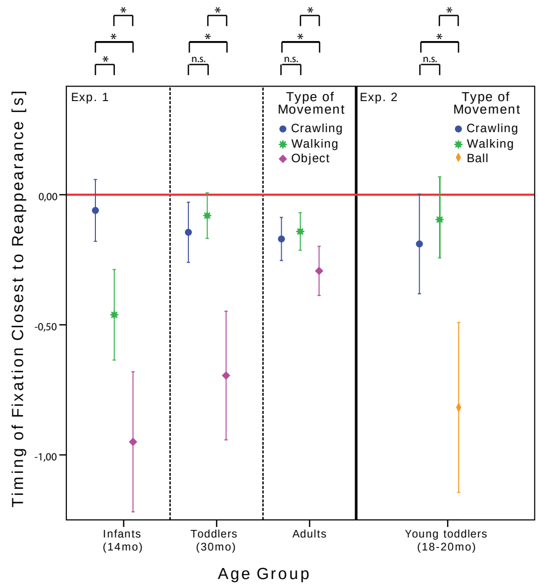

Figure 2: Action prediction accuracy: difference in time between gaze arrival at the post-occluder area and the time of actual reappearance, split by age group and type of observed movement. Bars represent 95% confidence intervals around the means.

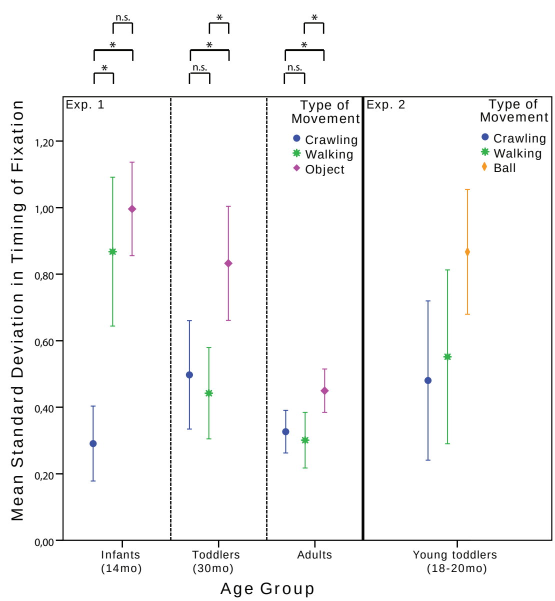

Figure 3: Action prediction stability: standard deviation of the difference in time between gaze arrival at the post-occluder area and the time of actual reappearance per participant and per type of observed movement. Bars represent 95% confidence intervals around the means.

Table 1: Results of the paired-samples t-tests used to examine the effects of age group on prediction accuracy. *) $p < 0.05$, **) $p \leq 0.01$, ***) $p \leq 0.001$.

Age Group	Crawling-Walking	Crawling-Object	Walking-Object
Infants	$t(15) = 3.27^{**}$	$t(15) = 6.44^{***}$	$t(15) = 2.52^{*}$
Toddlers	$t(22) = -0.95$	$t(22) =3.74^{***}$	$t(22) = 5.42^{***}$
Adults	$t(15) = -1.30$	$t(15) = 5.44^{***}$	$t(15) = 6.17^{***}$
All participants	$t(54) = 1.54$	$t(54) = 6.32^{***}$	$t(54) = 5.84^{***}$

Table 2: Results of the paired-samples t-tests used to examine the effects of age group on prediction stability. *) $p < 0.05$, **) $p \leq 0.01$, ***) $p \leq 0.001$.

Age Group	Crawling-Walking	Crawling-Moving object	Walking-Moving object
Infants	$t(15) = -4.66$***	$t(15) = -6.96$***	$t(15) = -1.06$
Toddlers	$t(22) = 0.47$	$t(22) = -2.49$*	$t(22) = -3.48$**
Adults	$t(15) = 0.64$	$t(15) = -3.95$***	$t(15) = -3.43$**
All participants	$t(54) = -1.91$	$t(54) = -5.42$***	$t(54) = -4.01$***

Table 3: Results of the independent-samples t-tests used to examine the differences between the age groups on Prediction Accuracy and Stability. *) $p < 0.05$, **) $p \leq 0.01$, ***) $p \leq 0.001$.

Age Group	Infants-Toddlers	Infants-Adults	Toddlers-Adults
Prediction Accuracy	$t(37) = -2.67$**	$t(30) = -5.05$***	$t(37) = -1.69$
Prediction Stability	$t(37) = 2.40$*	$t(23.5) = 6.91$*** [1]	$t(37) = 5.61$***

[1] In case equal variances could not be assumed as indicated by a significant outcome of Levene's test for equality of variances, adjusted dfs are reported.

DISCUSSION

Two main conclusions can be derived from Experiment 1. First, in accordance with what we had hypothesized, action prediction was more accurate and more stable for observed actions participants had more motor experience with. Second, in line with previous research, predictions of human movements were more accurate than predictions of non-human movements (Saunier et al., 2008; Stadler et al., 2012). In the following experiment, two factors were controlled for that might be criticized in Experiment 1. In Experiment 2, a more natural non-human control was used, namely video-recorded rolling balls. Furthermore, a critical age group of 18- to 20-month-old toddlers was included to test whether relatively little walking experience is sufficient to accurately predict walking.

Experiment 2

METHOD

Subjects

Eighteen infants between 18 and 20 months of age took part in Experiment 2. The sample consisted of 6 infants from each month cohort (11 females, mean age = 19.7 months, SD = 1.04). Two additional infants were recruited but data were not included in the analyses, due to technical failure (N = 1) or inability to walk (N = 1). The participants were recruited via the database of the Baby Research Center Nijmegen. Written parental informed consent was obtained prior to the study.

Procedure

The young toddlers first participated in an eye-tracking experiment with a procedure identical to Experiment 1. After the experiment, their walking proficiency was assessed. Children were asked to walk on a straight line of several meters, which had been set out on the floor using white tape (width of 1 cm) on the floor. The experimenter first demonstrated how to walk on the line by placing the feet sequentially on it and then invited the toddler to follow her example. A camera was positioned at the start of the line with the line in the middle of the field of view. Care was taken that the camera was positioned in the exact same way for each testing session. After administration of this walking task, parents filled in a questionnaire about the walking experience of their child, similar to the infant group in Experiment 1.

Materials

The walking and crawling stimulus videos of Experiment 1 were also used in Experiment 2. The object videos were replaced by videos displaying a rolling ball. The size of the ball in the video and occlusion duration were matched with the walking and crawling stimuli. Rolling balls were recorded against a green background and edited into the same background as the human movement videos (using Adobe Premiere Elements 11). Three different balls were used to match the different actors displayed in the human movement stimuli.

Results

The analyses of the gaze data were identical to Experiment 1. Repeated measures ANOVAs were conducted with Movement Type (crawling, walking, ball) as within-subjects factor. Movement type had an effect on prediction accuracy ($F(2, 32) = 10.2$, $p < 0.001$, , ηp = 0.39), with accuracy being higher for the two types of human movements compared to the ball movement, but not significantly different between crawling and walking (see Table 4 and Fig. 2). For prediction stability, no significant effect of Movement Type was observed ($F(2,24) = 1.49$, $p = 0.25$, see Fig. 3).

According to the parental report, the 14-month-old infants from Experiment 1 had significantly less walking experience (M = 1.8 weeks, SD = 3.2) than the 18- to 20-month-old toddlers from Experiment 2 (M = 23.9 weeks, SD = 8.4, $t(20.5) = -10.2$, $p < 0.001$). Age and walking experience appear to be closely linked in the young toddler group (r = 0.57, $p < 0.05$), whereas no such indication was found in the infant group ($p = 0.32$). No significant correlations were found between reported walking experience and prediction accuracy and stability of observed walking movements for either age group (ps > 0.2).

For the walking task, several indices were defined to describe the quality of the walking behavior. These indices were walking speed (number of steps divided by the time spent), the ability to walk on a straight line (ratio of steps on the line relative to the total number of steps taken) and step width (measured in pixels on the video-recording). These measures were based on items assessing walking skills from the Bayley Scales of Infant Development (van der Meulen, Ruiter, Lutje Spelberg, & Smrkovsky, 2000) and previous studies examining walking development (Adolph, 1997; Bril & Brenière, 1992). The indices of walking competence were not correlated with the amount of walking experience reported by the parents (ps > 0.30), nor were they correlated with the infants' age (ps > 0.27). Furthermore, the indices were not significantly related to prediction accuracy and stability of the observed walking (all ps ≥ 0.15).

Table 4: Outcomes of the paired-samples t-tests used to examine the effects of movement type on prediction accuracy. *) $p < 0.05$, **) $p \leq 0.01$, ***) $p \leq 0.001$.

Age Group	Crawling-Walking	Crawling-Rolling ball	Walking-Rolling ball
Young toddlers	$t(16) = -0.91$	$t(16) = 3.31$**	$t(17) = 4.09$***

DISCUSSION

Experiment 2 yielded two main findings. First, predictions of human actions were again more accurate than predictions of object stimuli, in this case naturally rolling balls. Hence, the possible alternative explanation, namely that object movements were less accurately predicted due to the low plausibility and unfamiliarity of the observed action, can be ruled out on the basis of the results of Experiment 2.

Second, the young toddlers of Experiment 2 were equally accurate in predicting walking and crawling, which replicates the pattern of results found in the older toddler group of Experiment 1. Apparently, toddlers become able to precisely predict walking actions between 14 and 20 months of age, which is the period during which they also learn to walk themselves. This provides further evidence that walking development and the development of prediction accuracy of others' walking movements goes hand in hand.

Interestingly, Experiment 2 provided no evidence for a correlation between walking experience, as measured in the lab or as reported by parents, and prediction accuracy, i.e., the indices of walking experiences were not significantly related to prediction accuracy and stability of the observed walking. Furthermore, walking proficiency as measured in the lab was not related to walking experience as reported by the parents. Evidently, longer walking experience does not necessarily automatically imply better walking skills. A longitudinal study may shed more light on the relation between walking development and the development of predicting observed walking, as a longitudinal study may partially rule out the large individual differences that now potentially obscure the relationship between walking and its prediction.

General discussion

The current study aimed to shine new light on the question whether the accuracy of action predictions depends on motor experience, and thus on the motor system. Four groups of participants that differed in motor expertise were assessed directly in terms of accuracy and variability of predictions of observed actions. The results showed that participants who were not yet experienced in walking, but who were proficient crawlers, were less stable and less accurate in their prediction of walking compared to crawling, whereas participants who were experienced walkers displayed no such differences. Regardless of age, participants were more accurate in their predictions when observing human movement compared to object movement. Moreover, this difference between human and non-human movements held both for objects that moved with constant velocity and for objects moving with a natural velocity profile.

The finding that human movements were predicted more precisely than different types of object movements is in line with previous research (Saunier et al., 2008; Stadler et al., 2012). Moreover, this difference was found both for unnatural but computationally simple object movements (Experiment 1) as well as for more complex, but natural movements (Experiment 2). Whereas the motor system can provide accurate predictions of human movements for which it contains forward models, it cannot provide accurate predictions of non-human movements. Presumably, predictions of the moving objects are generated in different brain structures, for instance in MST or MT (Newsome et al., 1985; Tanaka & Saito, 1989). Also, human movements are more socially relevant than object movements, and hence prediction accuracy might have decreased for the less relevant situations. Future research could focus on the role of task relevance for prediction accuracy.

Central to the study was the hypothesis that participants with different motor skills vary in their prediction accuracy of the respective motor acts. According to the simulation account (Wilson & Knoblich, 2005) the same mechanism for predicting the sensory consequences of one's own actions is used to predict actions of others. Our results lend support for this account, as infants performed worse at predicting an action they had little experience with (i.e. walking) compared to an action they were proficient in (i.e. crawling). Toddlers and adults, who had experience with either action, were equally good in predicting walking and crawling. Experiment 2 showed that also a younger toddler group was able to generate predictions for walking that were equally accurate as predictions for crawling. These young toddlers were closer in age to the infant group of Experiment 1, but comparable in their motor abilities to the toddler group of Experiment 1. The prediction accuracy results of this group matched those of the older toddlers of Experiment 1: both groups predicted walking as accurately as crawling. Apparently, in the time frame in which infants learn to walk independently, they also improve in prediction accuracy for walking actions when they observe them in others.

These findings are consistent with the study by Van Elk and colleagues (2008b), who showed that proficient crawlers with limited to no experience with walking activate their motor system more strongly when watching others crawling compared to walking. When acquiring a new skill, an infant might use a wide variety of motor commands to try to perform the intended action, and with experience, the only the most effective motor commands become established in the motor system (Hadders-Algra, 2000; Sporns & Edelman, 1993). These motor commands can then be used to simulate and predict these actions when they are observed being performed by others. Predicting an observed action facilitates understanding of the action (Ambrosini et al., 2013). In sum, experience with an action can thus lead to a better understanding of this action in others (Hunnius & Bekkering, 2014; Sommerville, Woodward, & Needham, 2005; Woodward, 1998).

The finding that motor expertise is beneficial for action prediction is in line with results of Aglioti and colleagues (Aglioti et al., 2008), who showed that basketball experts are better in perceiving whether basketball shots would be successful or not. Though studies investigating experts are essential for this line of research, the current study looks at effects of motor experience in the general population. This study is among the first to show that differences in predictive abilities are not unchangeable properties of specific populations, but predictive abilities change over the course of development as a result of developmental changes in motor experience. This is also emphasized by the fact that the youngest age group, having crawling as main modus of locomotion, almost outperformed the children who were 16 months older in terms of prediction stability for crawling actions.

In sum, the results of the present study show that action prediction is more accurate and more stable for movements that are within the motor repertoire of an observer compared to movements that are not. These results are in line with the simulation account (Wilson & Knoblich, 2005), which postulates that the kinematics of observed actions can be predicted by means of a simulation in the motor system. For predictions to be accurate, the observed action needs to be established in the motor system of the observer. Consequently, young children who acquire new motor skills may also become more proficient social action partners (Meyer, Bekkering, Haartsen, Stapel, & Hunnius, in press), as their motor experience may help them to predict their interaction partner's actions and accurately time their own actions in response.

Acknowlegdements

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Chapter 6

Fifteen-Month-Old Infants Use Velocity Information to Predict Others' Action Targets

Abstract

In a world full of objects, predicting which object a person is going to grasp is not easy for an onlooker. Among other cues, the characteristics of a reaching movement might be informative for predicting its target, as approach movements are slower when more accuracy is required. The current study examines whether observers can predict the target of an action based on the movement velocity while the action is still unfolding, and if so, whether these predictions are likely the result of motor simulation. We investigated the role of motor processes for velocity-based predictions by studying participants who based on their age differed in motor experience with the task at hand, namely reaching. To that end, 9-, 12-, and 15-month-old infants and a group of adults participated in an eye-tracking experiment which assessed action prediction accuracy. Participants observed a hand repeatedly moving towards and pressing a button on a panel, one of which was small, the other one large. The velocity of the reaching hand was the only cue for predicting which button would be the target of the observed action. Adults and 15-month-old infants made more frequent visual anticipations to the target button compared to the non-target button and were thus able to use the information in the speed of the approach movement for the prediction of the action target. The 9- and 12-month-olds, however, did not display this difference. After the eye-tracking experiment, infants' ability to aim for and press buttons of different sizes was evaluated. Results showed that the 15-month-olds were more proficient than the 9- and 12-month-olds in performing the reaching actions. The developmental time line of velocity-based action predictions thus corresponds to the development of performing that motor act yourself. Taken together, these data suggest that motor simulation may underlie velocity-based predictions.

Keywords: Action prediction; Infancy; Speed-accuracy trade-off; Motor system; Predictive Eye-movements

Based on: Stapel, J.C., Hunnius, S., & Bekkering, H. (in press). Fifteen-month-old infants use velocity information to predict others' action targets. *Frontiers in Psychology, 6* (article 1092).

Introduction

Predicting others' actions is crucial for social interactions to run smoothly (Bekkering et al., 2009; Sebanz & Knoblich, 2009). Anticipating which goal object an action partner will grasp, however, is complicated in a world full of objects. How do observers predict which object another person is reaching for? Motor theories of action perception suggest that the motor system is used to predict others' actions the same way it is used to predict the outcomes of one's own motor acts (Kilner et al., 2007; Prinz, 2006; Wolpert et al., 2003; Oztop, Wolpert, & Kawato, 2005). In accordance with this notion, a large body of literature shows that the motor system is not only active during action execution but also during the observation of others' actions (Hari et al., 1998; Rizzolatti et al., 1996b; Cattaneo et al., 2007), suggesting that similar processes are at work during observation and execution. Consequently, laws governing action production can be expected to also affect action perception. One of these laws is Fitts's law (1954), which describes that actions directed at small targets require more time to perform. Recent empirical findings illustrate that observers have expectations about the speed of an observed movement depending on the size of the target (Grosjean et al., 2007) and that these expectations follow Fitts's law. However, it is yet unclear whether this law is used to predict ongoing observed actions. If so, this would allow people to predict the target of a partner's actions when many potential targets are present. The first question of the current research was whether observers indeed can use the velocity of an action to *predict* whether an action is directed at a small or large object. The key advantage of action prediction over mere processing of completed actions is that prediction allows for smooth and timely social interaction (Bekkering et al. 2009; Sebanz & Knoblich, 2009). A second aim of the study was to investigate which mechanism underlies velocity-based predictions. Given the large body of literature suggesting that the motor system is involved in action prediction (Kilner et al., 2007; Prinz, 2006; Wolpert et al., 2003; Oztop et al., 2005) and prior empirical evidence that Fitts's law affects action observation (Grosjean et al., 2007; Eskenazi, Grosjean, Humphreys, & Knoblich, 2009), it is plausible that motor simulations bring about velocity-based predictions. As a second question we therefore examined cross-sectionally whether motor development goes hand in hand with the development of velocity-based predictions.

When acquiring a novel motor skill, the actor builds associations between the motor commands utilized and the effects of these motor commands as experienced via the sensory modalities (Kawato, 1999, Miall & Wolpert, 1996). At first, gaze is directed at the effectors (hands, fingers, feet) to monitor the results of the new motor commands (Sailer et al., 2005; Burton, Castle, & Held, 1964). With action proficiency, gaze will no longer be directed at the effectors, but at the target of the action (Sailer et al., 2005) and hence reveals the target of the ongoing action. Based on associations formed during the acquisition phase, a forward model of the action can be constructed, which allows the actor to predict the sensory consequences of an intended action ahead of time (Wolpert, 1997). The forward model becomes more fine-grained with increasing motor experience. In this way, motor experience leads to a precise forward model of the action and to precise predictions of future sensory states.

Motor theories of action perception assume that similar processes are active during action perception as during action production (e.g., Oztop et al., 2005). On a behavioral level, goal-directed eye movements have been shown to be predictive and follow the same time course for action execution and action observation (Flanagan & Johansson, 2003), and blocking the motor system by means of Transcranial Magnetic Stimulation (TMS) disrupts these predictive eye movements (Elsner, D'Ausilio, Gredebäck, Falck-Ytter, & Fadiga, 2013). Eye-tracking studies investigating the development of action prediction indicate that motor experience is crucial for predicting these actions in others (Falck-Ytter et al., 2006; Kanakogi, & Itakura, 2011; Ambrosini et al, 2013; Stapel, Hunnius & Bekkering, submitted). It is therefore likely to assume that velocity-based predictions become more accurate as a consequence of motor development.

In action performance, speed depends on the accuracy required for successful completion of the action. That is, the more accurate one has to be, the slower the movements become. Fitts (1954) formalized and quantified this relation based on data he collected, and the relation he found was shown to hold for many movements (see for an overview Plamondon & Alimi, 1997). Fitts's law states that the time needed to move between two targets is based on the distance between the targets and the width of the target (Fitts, 1954). Hence, movement time can be shorter between large compared to small target objects, and bridging small distances can be done quicker than bridging large distances. For example, reaching and grasping a small object requires more accuracy, and has been shown to take more time (Bootsma, Marteniuk, MacKenzie, & Zaal, 1994; Zaal & Thelen, 2005).

Empirical research shows that in adults, not only action production follows Fitts's law; also action perception is influenced by it. For instance, adults were capable of dissociating whether an observed, artificial reaching movement was physically possible or impossible in reality given the movement time, adhering in their judgments to Fitts's law (Grosjean et al., 2007). Also, a neurophysiological patient violating Fitts's law in his action production by not adjusting movement speed for smaller targets displayed similar violations in action perception (Eskenazi et al., 2009). This indicates that determining whether observed actions have an appropriate velocity might be grounded in the action production capabilities of the observer. Presumably, the neural motor system is recruited during action perception to simulate the observed action. These simulations during action observation may enable the observer to predict future states of the action (Wilson & Knoblich, 2005). An fMRI study by Eskenazi and colleagues (Eskenazi, Rotshtein, Grosjean, & Knoblich, 2011) revealed that activity in motor areas of the brain during the observation of movements was related to the difficulty of performing these movements as formalized in Fitts's law. In sum, the speed-accuracy trade-off not only constrains action production, it also affects action observation, and these constraints influence activity in motor cortical areas of the brain during observation and execution.

The current study was set out to investigate whether observers not only use the speed-accuracy trade-off to dissociate possible from impossible actions, but whether they also use this principle to predict the targets of actions they observe. Furthermore, if the motor system generates target predictions based on the velocity of the observed movements, then these predictions can only be made by observers capable of performing the observed action herself, because before skill acquisition, the observer most probably lacks the necessary forward model to predict the action outcome. We therefore adopted a developmental approach: Nine-, 12- and 15-month-old infants participated together with adults in an eye-tracking experiment during which they observed an actor moving her hand towards and pressing a large or a small button. In all stimulus videos, there were two buttons, a large and a small one, at the end of a table. A hand started moving from the one side of the table to the other to press either the large or the small button. If participants made more correct visual anticipations than incorrect anticipations, then that would indicate that the observers used the velocity of the hand to predict which button would be pressed. We hypothesized the ability to predict others' aiming and pressing actions to develop in parallel with their own ability to accurately aim their hand and finger at a small target in order to press it. Young infants might be able to successfully aim with their hand for a large button, but they might base their movements on a relatively inaccurate forward model, which prevents them from smoothly reaching for and pressing a small button. Having a coarse-grained forward model might necessitate them to make corrections in their movements if they would try to aim for and press a small button. At the same time, this coarse-grained forward model might not allow them to make accurate predictions of other's actions. To further clarify the role of motor expertise for velocity-based action prediction, the infant groups were tested for their ability to aim at a small button. This allowed us to disentangle whether potential developments in predicting targets based on speed arise specifically from the development of the motor skill at hand or rather reflect other age-related changes.

Method

Participants

Twenty-seven infants (8 girls) with a mean age of 8.8 months (SD = 0.3), 28 infants (16 girls) with a mean age of 12.2 months (SD = 0.3), and 28 infants (11 girls) with a mean age of 15.0 months (SD = 0.2) participated in the study. Furthermore, 18 adults (12 women, mean age = 24.9 years, SD = 5.2) took part in a longer version of the experiment. Eight additional infants (three 9-month-olds, five 12-month-olds) and one additional adult were tested but excluded from the analyses because they did not meet the eye-tracking calibration criteria (7 infants) or because they produced an insufficient amount of gaze data (gaze data for only 3 or less trials: 1 infant, 1 adult). All infant groups were recruited via the Baby Research Center in Nijmegen. The adults were recruited via a participant database of Radboud University Nijmegen. Written informed consent of the participants or the participants' parents was obtained prior to participation. Participation in the study was rewarded with a small gift (an infant book or 10 Euros for the participating infants, 5-Euro-gift vouchers or credit points for the adults). The study was approved by the ethical committee of behavioral science at the Faculty of Social Sciences in Nijmegen, and was conducted in conformity to the ethical standards of (developmental) psychology.

Stimuli

Four different short video clips (duration: 3.1 to 3.6 sec) were used as stimulus material. The videos showed a table with a large (4 by 4 cm) and a small (1 by 1 cm) button on one side (see Figure 1). An actor was sitting behind the table. One of the buttons was relatively close to the edge of the table, and the other one was a bit further away from the edge towards the middle. In half of the videos, the small button was the one closer to the edge of the table, whereas it was the large button in the other half of the videos. The stimulus videos started with a still frame in which the actor's hand was shown on the far side of the table. To create a balanced stimulus set, also horizontally flipped versions of the videos were made by means of editing the original video material in VirtualDub (www.virtualdub.org). After one second, the hand started moving towards the buttons, and the action ended with the hand pressing one of the buttons with the index finger. The video ended with one second of still frame of the hand in its end position with the index finger pressing the button. This could be either a small and far, small and close, large and far, or a large and close button. The index finger was already stretched out during the start of the movie, such that during movement the fingers did not move with respect to the hand. As expected based on Fitts's law, movements towards the small buttons took more time than movements towards the large buttons (300 msec difference), and pressing the distal button required more time than pressing the proximal button (20 msec difference). The main manipulation in the stimuli that affected the movement time was the size of the buttons and not the distance between the buttons. The reason for this choice was of practical nature: a large distance between the buttons would have meant that we would have had to reduce the distance between the initial hand position and the first target, which would have led to movement times too short to allow the participants to display a predictive eye-movement (data of 15-month-olds indicate that movement times of 800 msec are insufficient to allow the infant to make an anticipatory saccade based on kinematic information only, Stapel, Elsner, Galazka, & Gredebäck, unpublished results).

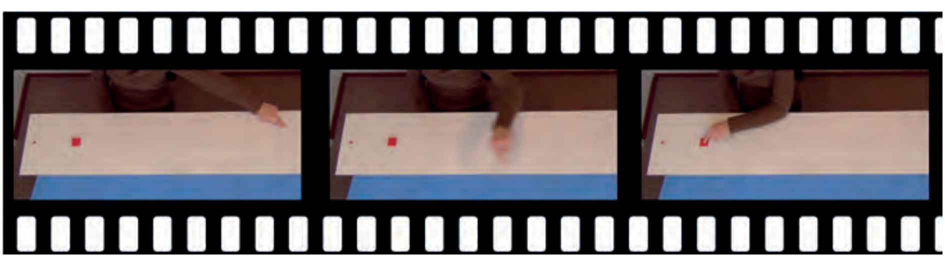

Figure 1: Example frames from a stimulus video with the small button close to the edge of the table and the hand moving to the large button.

Button press device

To assess the infants' proficiency of aiming at and pressing large and small buttons, a button press device was constructed (see Figure 2). The device consisted of a wooden frame, in which boards with a single, red button could be fitted. Two boards were used, one with a small (1 by 1 cm) button, and one with a large button (4 by 4 cm) in the middle of the board. The main factor influencing movement time in the observation task was button size and not distance. Therefore, only button size was manipulated in the execution task. To ensure that infants would aim precisely at the button instead of pushing it with their whole hand, the buttons were inlaid into the surface, with a black edge around them. Pressing elicited a sound to enhance infants' motivation to try to succeed in pressing the button.

Procedure

The procedure for data collection was kept as similar as possible across age groups. Participating infants were seated in a car chair resting on the lap of their

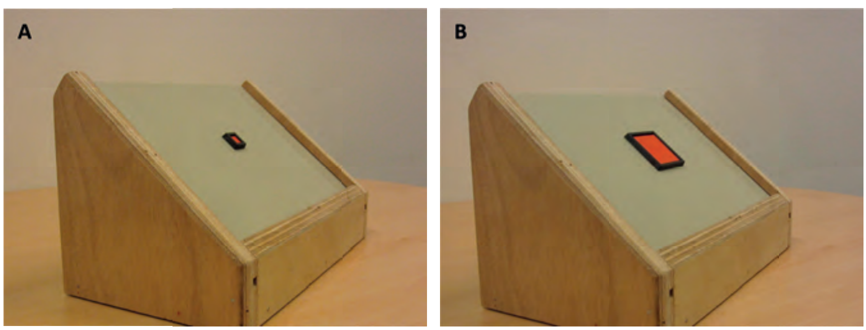

Figure 2: The button press device. The small button is presented at the left (A), and the large button at the right (B).

caregiver in front of a computer monitor. Participating adults were seated on an office chair adjusted to their height. Infants' gaze was recorded using a Tobii 1750 (Tobii Technology, Sweden). Adults' gaze was recorded with a different, but comparable eye-tracker (Tobii T120; Tobii Technology, Sweden), as adults were tested for a different, unrelated study at the same occasion. All participants first underwent a calibration procedure in which a contracting and expanding circle accompanied by a sound was shown on 9 locations on the screen, forming a 3-by-3 grid. The calibration was accepted, if data was available for 7 or more calibration points. Immediately after calibration, the experiment started, which consisted of 96 (adults) or 48 (infants) trials. Trials were presented in random order and were interleaved with brief attractive audiovisual clips to maintain the attention of the participants to the screen (16 for the infants, 3 for the adults).

After the eye-tracking experiment, infants who had been sitting in the car seat were put on their parents lap. They were presented with the button pressing device, which stood on the table in front of them. Their actions were recorded with a video camera (Sony handycam DCR-SR190, frame rate: 25 Hz). They were first asked to try to press the large button, then the small button, followed by again the large and then the small button. The experimenter demonstrated how to press the button and encouraged the infant to follow her example in case infants were hesitant to press the button themselves.

Gaze data analyses

Square-shaped areas of interest (AoIs) of equal size (100 by 100 pixels) were defined around the buttons in the stimulus displays, and in addition, an AoI was defined containing the full display of the stimulus movie (1280 by 580 pixels). First, the stimuli that were attended to were counted per participant and per condition. A stimulus was considered "watched" if at least one fixation fell on the full stimulus AoI while the stimulus video was playing. Second, per condition, trials were counted in which the participants fixated at one of the two button AoIs after onset of the hand movement and before the hand reached the AoI of the first button. These target fixations are subsequently referred to as "anticipatory looks". A percentage of trials in which participants showed an anticipatory look to one of the buttons was calculated based on the total number of watched trials in that condition. In trials in which participants looked at both buttons during the anticipation interval, the trial would count both as a target and a non-target anticipation. Repeated measures ANOVAs were used to investigate whether participants correctly predicted whether a button served as the target of the action or not.

Video coding of button presses

Infants' attempts to press the large and small buttons were coded from the video-recordings. Per type of button, the attempts to press the button were counted. Behavior was considered as an attempt to press the button if the infant's hand touched the board in which the button was embedded while the infant looked at the button. Button press attempts were considered successful if the infant touched the button while looking at it. Attempts in which the infant was being moved or helped by their caregiver were excluded from the analyses. Beside success on the task, we were interested in the quality of the infant's aiming. A well-aimed button press needs no correction in the movements, such that the aiming hand or finger lands directly on the button instead of first on the surroundings of the button. Movement correction was quantified as the time between the first moment the device was touched and the first moment the button was touched. Accurate initial aims would result in short (down to zero seconds) movement correction times.

Results

Action perception

The action in the stimulus display became disambiguated once the hand reached the first button, as then either the hand stayed on the first button, or continued to the second button. Thus, importantly, only anticipatory fixations initiated during this first ambiguous phase of the action were analyzed (the duration of the ambiguous phase ranged from 1.58 to 1.88 seconds after stimulus onset). An implication of this analysis choice was that fixations to the first button would likely occur more frequently compared to fixations to the second button, because for the latter, gaze needed to be more ahead of the action in space and time to reach the button during that period. Inspection of the data substantiated this assumption. Figure 3 displays the mean percentage of fixations to the first button (closest to the initial position of the hand) and the second button (further from the initial position of the hand) during the analysis window collapsed over conditions. Given that participants tended to anticipate only to the close button and appeared to exhibit hardly any anticipations to the far button, the subsequent conditional analyses will focus on anticipations to the first button, which was either the target of the action, or not.

A repeated measures ANOVA was conducted to analyze the frequency of anticipatory looks to the first button with button function as a within-subjects factor (target, non-target) and age group (9-month-olds, 12-month-olds, 15-month-olds, adults) as a between-subjects factor. There was a main effect of age on the percent-

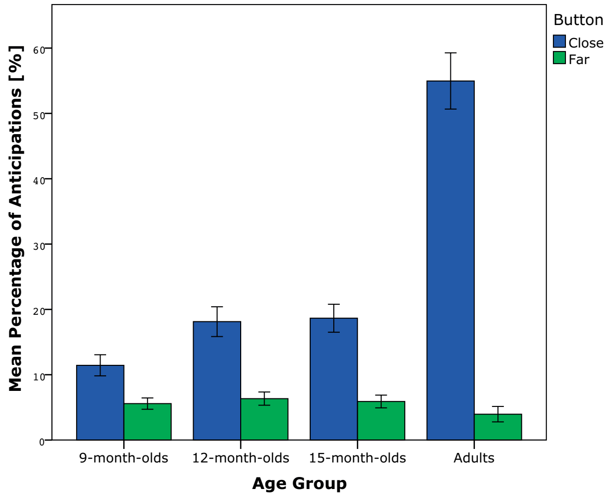

Figure 3: Mean percentage of visual anticipations to the button close or far from the initial position of the hand, regardless of condition, split by age group. Error bars represent one standard error of the means.

age of anticipatory looks ($F(3,97) = 50.33$, $p < 0.001$, $\eta^2_p = .61$). Post-hoc independent samples t-tests showed that adults displayed a higher percentage of anticipatory looks (M = 55%, SD = 18) than the 15-month-olds (M = 19%, SD = 11, $t(25.4) = 7.55$, $p < .001$)[3] and the 12-month-olds (M = 18%, SD = 12, $t(26.5) = 7.56$, $p < .001$). No difference was found in anticipatory looks between the 15- and 12-month-olds ($t(54) = 0.17$, $p = .867$). The 9-month-olds showed less frequent anticipatory looks (M = 11%, SD = 8) than the 12- ($t(53) = 2.38$, $p = .021$) and 15-month-olds ($t(53) = 2.68$, $p = .010$).

A main effect of button function was observed ($F(1,97) = 14.56$, $p < .001$, $\eta^2_p = .13$), indicating that across age groups, participants anticipated more frequently to the first button when it was the target (M = 25%; SD = 22) compared to when it was not the target button (M = 21%; SD = 19). A significant interaction effect was found ($F(3,97) = 5.09$, $p = 0.003$, $\eta^2_p = .14$), indicating that the age groups differed in the frequency of anticipatory looks to the target compared to the non-target button. To further verify that the interaction effect was not solely due to the difference between adult and infant performance, an ANOVA was run without the adult data. A marginally significant main effect of button function was found ($F(1,80)= 3.38$, $p = .070$, $\eta^2_p = .04$), together with a significant interaction effect of age group and

3 In case equal variances could not be assumed as indicated by a significant outcome of Levene's test for equality of variances, adjusted dfs are reported.

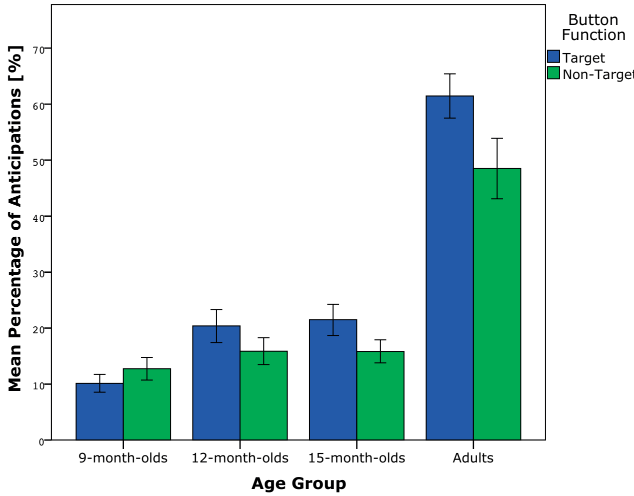

Figure 4: Percentage of anticipatory looks to the first button when it was the target (blue bars) or not (green bars) split by age group. Error bars represent one standard error of the means.

button function ($F(2,80) = 3.51$, $p = 0.035$, $\eta^2_p = .08$). Planned paired comparisons for the separate age groups revealed that adults anticipated more frequently to the button when it was the target compared to when it was not ($t(17) = 3.32$, $p = .004$). The same was the case for the 15-month-olds ($t(27) = 2.37$, $p = .025$), whereas the 12- and 9-month-olds did not look more frequently at the first button when it was the target compared to when it was not (12-month-olds: $t(27) = 1.59$, $p = .125$, 9-month-olds: $t(26) = -1.45$, $p = .141$; see Figure 4).

Action production

A repeated measures ANOVA was used to analyze the effect of button size (small, large) and age group (9-month-olds, 12-month-olds, 15-month-olds) on the percentage of successful button press attempts out of all attempts. A main effect of button size on the percentage of successful button presses was found ($F(1,68) = 28.05$, $p < 0.001$, $\eta^2_p = .29$), indicating that the infants were more successful in pressing the large ($M_{large} = 88\%$, $SD_{large} = 22$) compared to the small button ($M_{small} = 69\%$, $SD_{small} = 37$). Furthermore, the interaction between age group and button size was found to be significant ($F(2,68) = 15.18$, $p < 0.001$, $\eta^2_p = .31$). Independent samples t-tests showed that the 12-month-olds were more successful than the 9-month-olds when trying to press the small button ($t(32.9) = 5.79$, $p < 0.001$), but no significant differences were found between these groups when trying press the large button ($t(42) = 0.51$, $p = 0.611$). The success rates of the 12-month-olds for the small and large button ($M_{small} = 86\%$, $SD_{small} = 19$, $M_{large} = 88\%$, $SD_{large} = 24$) were not different from the 15-month-olds ($M_{small} = 81\%$, $SD_{small} = 35$, $t(47) = 0.65$, $p = .522$; $M_{large} = 90\%$, $SD_{large} = 26$, $t(48) = -0.29$, $p = .771$). In addition, the percentage of successful button presses was found to be higher in general for the 12- compared to the 9-month-olds ($F(2,68) = 15.18$, $p < 0.001$, $\eta^2_p = .31$; 9-month-olds: $M_{small} = 38\%$, $SD_{small} = 34$, $M_{large} = 85\%$, $SD_{large} = 12$).

An identical repeated measures ANOVA was conducted on the movement correction time data. A main effect of button size was observed ($F(1,63) = 53.81$, $p < 0.001$, $\eta^2_p = .46$), as significantly more time was needed to correct the aiming movement to a small ($M_{small} = 0.52$ sec, $SD_{small} = 0.54$) than to a large button ($M_{large} = 0.08$ sec., $SD_{large} = 0.14$). The interaction between age group and button size had a significant effect on the movement correction times ($F(2,63) = 6.69$, $p = .002$, $\eta^2_p = .18$). The three age groups were equally fast in pressing the large button ($M_{9mnts} = 0.09$ sec, $SD_{9mnts} = 0.12$, $M_{12mnts} = 0.10$, $SD_{12mnts} = 0.12$, $M_{15mnths} = 0.06$, $SD_{15mnths} = 0.18$, all ts < 1.0, all ps > .308). However, the 15-month-olds needed less time for correcting their movements than the other two groups when aiming for the small button ($M_{9mnths} = 0.82$ sec, $SD_{9mnths} = 0.79$, $M_{12mnths} = 0.50$ sec, $SD_{12mnts} = 0.32$, $M_{15mnts} = 0.27$ sec, $SD_{15mnths} = 0.15$; ts > 3.0, ps ≤ 0.006), whereas the 9- and 12-month-olds differed only marginally in this respect ($t(26.8) = 1.71$, $p = .099$). Furthermore, movement correction time was dependent on age ($F(2,63) = 6.93$, $p = .002$, $\eta^2_p = .18$), which was caused by differences in aiming for the small button.

Relation between action observation and action production

The results presented above show that success rates in aiming at the small button improved between 9 and 12 months of age and movement correction times decreased between 12 and 15 months of age. The ability to make velocity-based predictions develops in parallel, as 15-month-olds displayed velocity-based predictions, whereas 9- and 12-month-olds did not. To study the relation between action observation and action performance more closely, we examined the group of 12-month-olds, as this was the transitional group consisting of infants who were at the verge of learning to use velocity to predict actions. A correlation analysis was performed to investigate whether action production and action prediction skills were related at the level of the individual infants. In the correlation analyses, proficiency in aiming at the small button was used as the measure of interest, as this reflects the ability to aim with high precision best. The time needed to correct the aiming movements to the small button was not found to be related to the prediction accuracy, expressed as the difference between the percentage of target and non-target anticipations (p = .654, controlling for age in days). Likewise, the relation between the success rate of aiming at the small button was not found to be related with action prediction accuracy (p = .902, controlling for age in days).

Discussion

The aim of the current study was to examine whether the velocity of a movement is used by an observer to predict which object will be the target of the observed action, and if so, whether motor development and hence the motor system is crucial for these predictions to emerge. Gaze data showed that adults and 15-month-old infants more frequently displayed visual anticipations to a button when it was the target compared to when it was not. This indicates that they based their predictions on the speed of an observed movement, as velocity was the only cue available for distinguishing targets from non-targets. In contrast, infants of 9 and 12 months of age did not show any indications that they used the speed information of the observed movement for their action predictions. This was congruent with the development of producing this action: 15-month-olds were more proficient in aiming at and pressing a button accurately than the 12- and 9-month-olds. This suggests that the motor system underlies velocity-based predictions.

Three factors influenced how frequently the observers looked at the buttons while the action was unfolding. First, many more anticipatory looks were made to the button nearest to the initial position of the hand than to the button located further away, when the hand had not yet passed the nearest button. However, our analysis period ended when the hand was at the point of passing the nearest button, because once the hand had passed the first button, it was obvious that the second button was the target. As a consequence, to be counted as a predictive look, observers had to be more ahead of the action when predicting the far button than when predicting the near button. Due to the low base rate of predictions to the far button, only the predictions to the first button could be analyzed.

The second factor that influenced anticipatory looks was the velocity of the movement, which was the main manipulation in the current study. The results showed that participants looked more frequently at the first button when it was the target compared to when it was not, which indicates that the participants made use of the velocity information of the hand to predict which button would be pressed.

The third factor that affected the frequency of anticipatory looks was age. Whereas adults and 15-month-old infants looked more frequently to the first button when it was the target compared to when it was not, 9- and 12-month-old infants did not show this difference.

Velocity-based predictions may result from action simulation in the motor system of the observer. The motor system has been shown to respond stronger to the observation of actions that have to be performed with more accuracy (Eskenazi et al., 2011). The speed people expect to see during an observed action matches the the actual speed of the performed action (Grosjean et al., 2007; Eskenazi et al., 2009), which illustrates that the action-perception link also plays a role in the speed-accuracy trade-off (Flanagan & Johannson, 2003; Hari et al., 1998; Rizzolatti et al., 1996a; Cattaneo et al., 2007). Given these prior findings, the hypothesis of the current study was that the motor system not only underlies post-hoc judgments of the observed velocity of movements, but also facilitates on-line predictions made while the action still unfolds. Our results are in line with this hypothesis: The action prediction performance of the 15-month-old infants suggested that they use velocity information in action prediction, whereas the 9- and 12-month-olds seemed not to integrate the observed velocity in their predictions of the observed actions. The tested 15-month-old infants were also better at pressing buttons than the 9- and 12-month-olds. Using velocity information to predict which button will be pressed thus follows – at least by and large – the same developmental time course as the ability to press buttons. However, within the group of 12-month-old infants, the individual button pressing proficiency was not found to be related to the ability to use speed for action prediction. It might well be that our motor measurement was not sensitive enough to correlate motor performance with action prediction performance at an individual level. Nevertheless, it is interesting that the differences in motor performance at the group level overlap with the anticipatory eye capacities in the observation task. However, at least two alternatives can be given for the suggested improvement in terms of motor simulation. First, visual experience acquired between 12 and 15 months of age may contribute to velocity-based predictions as well (Hunnius & Bekkering, 2014). Second, the effects observed could also be related to a general maturation pattern of the brain that enables both action execution as well as action observation. The importance of visual experience and brain maturation in the development of velocity-based predictions can be tested in future research by investigating whether 15-month-olds can use velocity information for the prediction of actions that are not yet part of their motor repertoire.

In conclusion, we found empirical evidence that observers can predict the target of an action based on the velocity of the observed movement. In the current study, the action target was a button. Fifteen-month-old, but not 9- and 12-month-old infants showed an adult-like prediction pattern, suggesting that at 15 months of age, infants are beginning to use velocity to inform their predictions of other's button pressing actions. The 15-month-olds were more proficient in performing this type of action compared to the 9- and 12-month-olds. Together, this indicates that the development of velocity-based predictions follows a time line corresponding to the development of motor skill of the predicted action. Future research should parse out the roles of visual and motor experience for action prediction. Being a proficient actor may turn out to be necessary in order to accurately predict what other people are planning to do.

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Chapter 7

General Discussion

The prediction of others' actions is fundamental for understanding others' behavior and for selecting an appropriate response (Castelfranchi, 1998; Vesper, Butterfill, Knoblich, & Sebanz, 2010). This thesis describes a series of studies that investigated which types of information are used to predict others' actions and from which age infants make use of these types of information to predict others' actions. Furthermore, the studies were aimed to unravel the processes underlying action prediction development and, at the same time, unravel the processes underlying human action prediction in general. In this last chapter, the findings from the previously described five empirical studies and their implications for our understanding of action prediction in infants and adults are discussed.

Summary of the main findings

Types of information

As outlined in the General Introduction, actions contain multiple sources of information that can be used either separately or in combination to predict future states of an observed action. Potential sources investigated in the current thesis are object-knowledge, the presence of a distinct action target, the context of the action, and the kinematics of the actor. Starting with object-knowledge, a previous eye-tracking study had shown that the frequency with which the end-location of an action is predicted by infants and adults depends on the object that is being used (Hunnius & Bekkering, 2010). For instance, a phone rather than a cup is predicted to go the ear and a cup rather than a phone is predicted to go to the mouth. Chapter 2 showed that the neural responses to observation of these more and less predictable object-directed actions were different, which provides further evidence for the claim that object-knowledge plays a role in predicting actions.

Moreover, the results reported in Chapters 2, 4, 5 and 6 illustrate that infants and adults are able to predict the object or end-location an action is targeted at. Object-directed actions turned out to be more predictable than not object-directed actions (Chapter 3). However, follow-up experiments presented in Chapter 3 highlighted that object-directed actions may be more predictable because actors tend to move in a more predictable manner when they move towards a target object compared to when their movements are not object-directed. This only held if the action was constrained by the context, suggesting that the combination of having a spatially defined action target and having to take into account barriers reduces the degrees of freedom of the movements to an extent that the action becomes clearly more predictable.

The role of kinematics for action prediction was investigated in more depth in the experiments presented in Chapter 5. There, the prediction accuracy of the timing of movements was assessed. Observers were to base their predictions on different types of movements, such as walking and crawling, or the movements of objects. Prediction accuracy was higher for observed human compared to object movements. Furthermore, the youngest infants (14-month-olds) were more accurate in predicting the timing of crawling than of walking, indicating that movement type affects action prediction.

The impact of kinematics on action prediction was studied from another angle in Chapter 6. Infants and adults observed object-directed actions with different velocities. The results showed that velocity of the movements is used in action prediction.

Developmental timeline

The different types of information that are used in action prediction might not be integrated into infants' action prediction all at once, and studying the developmental timeline of action prediction may offer insight in how different capacities build on each other. In addition, such a developmental timeline might provide indications about the developmental processes underlying action prediction development, and at the same time, give insight into the processes underlying action prediction in general.

To start again with object-knowledge, previous work had shown that by 6 months of age, infants can already make target predictions based on the objects involved in an action (Hunnius & Bekkering, 2010). By that age, infants are not yet capable of performing at least part of the observed actions (e.g., bringing objects to their ears), which rules out the possibility that motor experience underlies these predictions. An inborn notion of how artifacts are normally used also seems highly unlikely. Quite plausibly, these predictions might thus be acquired through observational experience. Despite the fact that early predictions of object use are based on knowledge that is most likely acquired through visual experience, we observed in Chapter 2 that at 12 months of age, the motor system is active during object-based predictions. At this age, infants are capable of performing the observed actions, as caregivers of the participating 12-month-olds reported that their infant performed this type of action in daily life. Together, these studies suggest that although predictions may first be based on visual experience, once motor experience is acquired, the motor system may be used in predicting the actions as well.

Predictions about the timing of crawling actions were demonstrated to be accurate from at least 14 months of age, younger infants were not tested here (Chapter 5). Between 14 and 20 months of age, infants appear to become more accurate in predicting the timing of observed walking actions (Chapter 5). The 20-month-old participants had longer walking experience than the 14-month-olds according to caregivers' report. Predicting aim-for-and-button-press actions followed a different developmental time line: Fifteen- but not 12-month-old infants were shown to be able to predict the target of button-pressing actions based on the velocity of the hand aiming for the button (Chapter 6).

Processes underlying action prediction and action prediction development

Which processes underlie action prediction and its development? This question is discussed in almost every chapter of this thesis. My core hypothesis was that own action experience ameliorates the precision of action prediction. The results suggest that action experience indeed plays an important role in action prediction development. Prediction accuracy was found to be higher for actions observers had in their motor repertoire compared to actions not yet acquired (Chapters 5 and 6). Prediction of button-presses was shown to develop between 12 and 15 months of age, corresponding to the developmental timeline of becoming able to execute these button-pressing actions (Chapter 6). Fourteen-month-old infants capable of crawling were demonstrated to reach adult-levels of accuracy for predicting the timing of crawling (Chapter 5). Twenty-month-old toddlers, who were capable of both, crawling and walking, displayed equally accurate predictions for walking and crawling, whereas the 14-month-olds were less accurate in predicting walking compared to crawling. These findings support the idea that motor processes are crucial for action prediction (see also Chapter 2), in infants as well as in adults. Furthermore, these findings lend support for the notion that motor experience is fundamental for action prediction development.

In the remainder of this chapter, I discuss how our findings can be placed in the theoretical framework presented in the General Introduction, and what the implications of our findings are for existing theories on action prediction. To start, I show that the relative importance of goals compared to means for action prediction must be reconsidered. Movements form a key aspect in action prediction. Furthermore, I show that action prediction could theoretically be based on visual experience only, but that the empirical data shows otherwise, namely that motor experience crucially affects action prediction. I argue that motor experience has a unique and powerful contribution to action prediction beyond visual experience only. That is, motor experience can lead to more precise predictions and the computational models required for accurate action prediction can more easily be acquired through motor experience. First, I focus on action prediction itself and then on the processes underlying action prediction and its development.

What types of information are used to predict others' actions?

Actions consist of several elements that can be used to predict others' actions: the agent, the target, the movements, and the action context.

The agent

The potential effect of the type of actor is only briefly touched upon in the current thesis. In Chapter 5, observers had to predict the timing of objects moving with constant velocity (Experiment 1) and had to predict the timing of a naturally rolling ball (Experiment 2). From the viewpoint of agency ascription, the latter contains less agency cues, as the rolling ball was not self-propelled (Premack, 1990). The ball only lost movement energy along the way, in contrast to the objects that moved with constant velocity. Based on the data, it seems that agency ascription does not impact the prediction of the timing of object movements, as prediction accuracy for both actions is relatively low, but as the study was not designed to answer this question, the data do not directly speak to the agency issue. The role of agency cues in action observation is more elaborately debated by Turella and colleagues (Turella, Erb, Grodd, & Castiello, 2009) and Daprati and colleagues (Daprati et al., 1997).

The target

The infants and adults in our studies were able to identify potential targets in the actions they observed, as in many cases participants were found to look at the target location of the action (e.g., an area of the face or an object in the scene) before the action was completed (see Chapters 2, 4, 5, and 6). Action prediction accuracy was found to be higher for object-directed compared to not object-directed actions (see Experiment 1 of Chapter 3). The follow-up experiments described in the same chapter stress the need to consider not only the action targets when investigating action prediction, but also the information which comes from the actor's movements.

The movements

Theoretically, movements can be considered to be of less interest than goals, as the same goal can be reached through many different movements (Park, Kim & Nagai, 2014; Wolpert, 1997). In principle, observers do not need to take into account the details of the actor's movements, as long as the movements do not deviate from what would be expected based on the inferred target. The empirical results described in Chapter 3 suggest otherwise. Predictions of object-directed actions were more accurate than those of non-object-directed actions. Even without visual access to the target object observers were more accurate in predicting object-directed compared to not object-directed actions, suggesting that the actor's movements carried crucial information about the presence or absence of the target object.

Goals versus means

During the last few decades, the notion prevailed in the literature that goals (in the current thesis called 'action targets') are more informative for action perception and prediction than means (here called 'movements'; Umiltà et al. 2008; Grafton & Hamilton, 2007; van Elk et al., 2008a). Movements are thought to be relatively uninformative for action prediction because the relation between targets and movements can be expressed as a many-to-many mapping (Kilner et al., 2007; van Rooij et al., 2008). Many movements can be used to arrive at the same target, and the same movement may have many targets. However, the current data, alongside recent other empirical work (Becchio et al., 2008, 2012; Ansuini, Santello, Massaccesi, & Castiello, 2006; Ansuini, Giosa, Turella, Altoè, & Castiello, 2008; Sartori, Becchio, Bara, & Castiello, 2009; Schuboe, Maldonado, Stork, & Beetz, 2008), potentially indicate something else: although a target may be reached by many different movements, one movement may be associated to a single target. This changes the computational problem from a many-to-many mapping into a many-to-one mapping. If the action context and principles of efficiency further narrow down the solution space from many-movements-to-a-single-target into a selected-set-of-movements-to-a-single-target, then the problem of explaining action prediction becomes substantially smaller.

The action context

The context in which movements are performed is crucial for the interpretation of the action (e.g., Blakemore, Goodbody, & Wolpert, 1998; Iacoboni, 2005). Action constraints are a specific and clear case of how the context of an action influences the movements of the action. Barriers make a detour meaningful, but when the barrier is taken away, efficient actors should chose a new action path (Gergely & Csibra, 2003) if they want to preserve time and energy (Nelson, 1983). In Chapters 3 and 4, observers were asked to predict constrained and unconstrained actions. The results of these chapters are inconclusive about the impact of action constraints on action prediction. Chapter 3 showed that actors move in a more predictable way when facing an action constraint than in the absence of constraints, and in that way, action constraints support action prediction. Whether or not action constraints themselves are used for action prediction is yet unclear. Constraints have the potential to affect action prediction, but maybe constraints only affect local predictions, concerning the movements of the actor, and not global predictions about the final target of the action.

Processes underlying action prediction and the early development of action prediction

A question central to the current thesis is how action prediction develops and which processes underlie action prediction and its development. To what extent is action prediction development an experience-independent or a experience-dependent process? And if experience plays a crucial role in action prediction development, what aspects of these experiences make these experiences so valuable?

Is action prediction development experience-independent?

To make a clear case for an experience-independent viewpoint, it is necessary to test neonates and show that action prediction abilities are inborn. However, even if neonates are studied, still a case for experience dependency can be made (see e.g., Meltzoff & Moore, 1997), as sensorimotor experiences with actions can be acquired already in the womb. The current set of studies is therefore not well suited to make claims about the experience-independent nature of action prediction development.

There are two aspects in the current thesis that should be considered when discussing experience-independent processes in action prediction. First, for those favoring experience-independent theories, the current thesis provides some positive news. In line with experience-independent viewpoints, no evidence for a direct relation between motor experience and action prediction was found in Chapter 5 and 6. However, the absence of evidence does not allow the conclusion that the relation does not exist. Other related studies have found a relation between motor experience and action prediction (Kanakogi & Itakura, 2011; Gredebäck & Kochukhova, 2010; Ambrosini et al., 2013).

Second, experience-independent processes might bring about action efficiency, which is discussed in the current thesis. The naïve theory of rational action, an example of an experience-independent account, suggests that action targets can be predicted based on situational constraints and the path of an action, namely by assuming that actors strive for efficiency (Gergely & Csibra, 2003). In Chapter 4, action constraints were either present or absent, while the movements of the actor were held constant. Consequently, half of the actions were an efficient means, and half of the actions were an inefficient means to obtain the target object. Action efficiency had no significant effect on target predictions, contrary to what would be expected based on rationality theory.

Is action prediction development experience-dependent?

As discussed in Chapter 1, both visual and motor experience might contribute to action prediction development. From a theoretical perspective, it may be valuable to consider whether visual and motor experience have separate contributions to action prediction development. In practice, visual and motor experiences often coincide: normally developing infants observe the consequences of their own actions while they gain motor experience with new actions. For conceptual clarity, I will first separate these two types of experiences.

Visual experience

The case for a 'visual experience only' account: theoretical considerations

It is good scientific practice to generate and test minimalistic theories to explain phenomena. Parameters should only be included if necessary, a principle that is commonly known as Ockham's razor (Thorburn, 1915; Baker, 2003). For theory construction it is therefore valuable to evaluate to what extent action prediction development can *theoretically* be explained based on visual experience only. This theoretical excise will provide more insight into the benefits of visual experience and the limitations of visual experience for action prediction development.

In the first year of life, infants have limited motor capabilities (Thelen, 1995). The oculomotor system forms an exception, as it develops very early and is one of the first systems in development that reaches an adult level of functioning (Hunnius, 2007). As a consequence, visual experience can form the basis of action prediction development from earlier on than motor experience can. Infants may learn to predict others' actions through statistical learning, with observations of actions as the material to learn from. There is empirical support for this notion: infants are capable of predicting actions they cannot perform yet (Hunnius & Bekkering, 2010), and infants were shown to be capable of predicting events, with actions as a subclass, based on the statistical structure of observed event sequences (Haith et al., 1988; Monroy et al., submitted).

It is very useful that actions can be predicted as a result of purely visual experience with actions, as this allows the prediction of many types of actions not (yet) acquired by the observer. It enables observers to predict human actions outside their motor repertoire. For example, it allows gymnastic fans to predict the actions of Epke Zonderland. It also enables observers to predict actions performed by non-human agents, as it, for instance, might allow the prediction of the movements of a bird (Hunnius & Bekkering, 2014).

In sum, visual experience has several advantages over motor experience for action prediction development: 1) visual experience *can* and *does* affect action prediction *earlier* in development than motor experience can, 2) visual experience enables the prediction of a large range of actions that are not necessarily part of the observer's motor repertoire. But can the empirical data of the current thesis be explained by a 'vision only' account?

Can visual experience alone explain the empirical data?

A short tour through the empirical chapters of this thesis illustrates that visual experience alone cannot fully explain action prediction development. In Chapter 2, stronger motor activation was found during the observation and prediction of unusual compared to ordinary actions. Had the predictions been generated purely based on visual experience, then there was no need for the observers' motor systems to respond differently to usual or unusual actions. In Chapters 3 and 4, the effect of the presence or absence of action constraints on action prediction was measured. More specifically, the participants observed an actor turning from walking to crawling because the spatial location of the target object was not accessible by walking. Predictions were found, despite the fact that this type of action is rarely encountered. Because these actions are rarely observed in others, it is unlikely that visual experience forms the basis for prediction of these specific actions. In Chapter 5, observers were to predict the timing of walking and crawling movements. The results showed that not-yet-walking infants were more accurate in predicting the timing of other infants' crawling compared to walking. If observational experience were to be the only basis for action prediction, then the opposite pattern of results could have been expected, as walking is encountered more frequently than crawling. In sum, the empirical findings show, in contrast to what theoretically might be expected, that visual experience alone cannot fully explain action prediction development.

Motor experience

As visual experience alone cannot fully account for the present data, it is worth investigating whether inclusion of an additional factor, namely motor experience can lead to a more complete account of action prediction development. Can a motor account explain the empirical data?

Can motor experience explain the empirical data?

The present set of experiments is line with a motor account of action prediction and action prediction development. Chapter 2 showed that the motor system of 12-month-old infants was activated during action observation, which can be taken as an indication that the observed acts were simulated within the motor system. Moreover, the motor system was more strongly activated during the prediction of unusual compared to ordinary actions, suggesting that the motor system responds differently to predictable compared to less predictable actions. Chapter 5 showed that participants were more accurate in predicting the timing of actions that were in their motor repertoire compared to actions that were not. Chapter 6 showed that only infants and adults who were capable of performing the observed action were also capable of dissociating which would be the target of the observed action. In sum, the empirical data provided in this thesis show that motor experience and motor processes support action prediction development.

The case for a 'motor experience' account: theoretical considerations

The present data thus suggest that motor experience, together with observational experience, underlies action prediction development. However, as young infants have limited action capabilities, predictive processes based on motor experience may come available later than processes based on visual experience. What can be the benefits of developing a second, alternative mechanism to predict other's actions? Are there benefits? The perception-action link, which provides a good explanation for the effect of motor experience on action prediction, may also just be a byproduct of own action development (Heyes, 2010). The current thesis provides empirical support for the notion that motor experience has a unique and powerful contribution to action prediction development. There are at least three ways in which motor processes are of added value for action prediction beyond what can be obtained by purely visual processing.

First, motor experience may improve motor simulations (Wilson & Knoblich, 2005), such that more experience leads to more accurate simulations, which may produce predictions that are more accurate than those based on visual experience. Walking and crawling were equally well predicted by observers capable of both actions (Chapter 5), although crawling is less often observed in daily life, which implies that observers had less visual experience with this action than with walking. Moreover, the participating infants who were not yet capable of walking but capable of crawling were more accurate in their predictions of crawling than of walking. Thus, motor experience enables accurate predictions about the timing of observed actions.

Second, motor experience may lead to simulations that can help to disentangle what will be the target of the observed action if multiple targets are present. Data in Chapter 6 illustrated that participants were more accurate in predicting what would be the target of the action if the observed action was within their motor repertoire. Thus, motor experience enables observers to make more accurate target predictions.

Third, motor experience can serve as a powerful tool to discover the possibilities and impossibilities of the motor system and consequently the range of possible actions that one can generate. Similarly, exploring the motor capabilities also may lead the motor system to learn motor laws and may provide the actor with information about how to deal with situational constraints (Blakemore et al., 1998). The acquired 'motor knowledge' can in turn be used for action prediction (Blakemore et al., 1998). This 'knowledge' may also be acquired through visual experience. However, if visual experience is the basis for learning motor laws for the prediction of others' actions, then more instances of the actions are needed compared to a situation in which these laws are acquired through own motor experience. The perceived instances will namely stem from multiple individuals and will hence contain more variance than the instances of own actions, as individuals vary in their movement patterns (Cutting & Kozlowski, 1977; Loula, Prasad, Harber, & Shiffrar, 2005). The other side of the coin is that own motor experience offers less variability and therefore lower generalizability. Another advantage of relying on motor experience is that healthy individuals in general have more opportunities to perform actions than to observe them in others, because regardless of the situation, the self is always present, the availability of observable others may fluctuate. Moreover, infants seem to have the tendency to explore their capabilities and try different versions of the same action rather than to stick to the first solution that works for them (Adolph et al., 2012; Comalli, Abraham, Keen, & Adolph, in prep.). This motor exploration behavior gives them ample opportunity to acquire robust forward models that can be applied in many situations. Through action experience, observers might thus become sensitive to subtleties of movements performed by others. The data presented in Chapters 2, 3, 5, and 6 are in line with the notion that observers are sensitive to the details of other's movements. Chapters 5 and 6 show that motor experience enables observers to base their predictions on the movements of observed actions. Results reported by other labs point in the same direction. For instance, expert basketball players were found to be more accurate compared to visual experts and novices in dissociating whether a shot would be in or out, when presented with the first few video frames of a basketball shot (Aglioti et al., 2008). In a similar vein, expert basketball players have been demonstrated to be more accurate than novices at detecting deceptive basketball moves when presented with only kinematic cues of those movements (Sebanz & Shiffrar, 2009). Our studies illustrate that the same principles hold in early development and that these principles can explain the development of action prediction.

Directions for future research

Although a motor simulation account can explain action prediction and its development, it also raises some questions. These questions need to be addressed to come to a better understanding of processes underlying action prediction and action prediction development.

Predicting movements and predicting action targets

According to motor simulation accounts, action targets are predicted based on the observed movements, and simultaneously, movements are predicted based on the action target (Prinz, 2006; Kilner et al., 2007; Schubotz & von Cramon, 2008). How can both of these statements hold? There are two potential explanations which are not mutually exclusive. The most commonly mentioned explanation is that both forward and inverse models are employed by observers to predict movements and action targets (Wolpert et al., 2003; Kilner et al., 2007; Miall, 2003; Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003). An inverse model can run on a part of the observed movements to detect what the potential action target could be given these movements, and after a hypothesis has been formed about the potential target, forward modeling can be used to predict how the movements should unfold given the inferred target (Oztop et al., 2005).

The second explanation includes, besides motor aspects, higher-order cognitive processing to explain action prediction (Csibra, 2007; Ansuini et al., 2014). According to this explanation, actions can be segmented into distinct periods of time. Before movement onset, the observer might identify aspects crucial to the action, for instance the action context, and the posture of the actor. Basic perceptual processes might serve to identify edges, depth cues, surfaces, and might lead to the identification of objects (Spelke, 1990; Gerlach & Marques, 2014). More advanced processes, probably relying on previously acquired knowledge, determine the presence of potential actors, and might, for instance based on the distance between the actors and the objects present in the scene, start selecting objects as potential action targets. Potential targets may need to be within reaching distance of the actor (Makin, Holmes, & Ehrsson, 2008; Caggiano, Fogassi, Rizzolatti, Thier,

& Casile, 2009) and should afford manipulation. Implicit action knowledge about these affordances (Gibson, 1977) might be acquired through observational or active experience. Once the movement starts, some of the potential targets can be ruled out. The direction of the movement might serve as a strong cue to which of the many objects is the target. From that point onwards, simulations can start based on how the observer would perform the movements required to attain the now inferred target.

Although the first explanation can account for the data presented in Chapters 5 and 6, it cannot explain the findings described in Chapters 2 and 3. That is, previously acquired knowledge about objects and situational constraints affected the observer's action predictions, which can well be explained by the second explanation, which includes higher-order cognitive processing. More specifically, in the study presented in Chapter 2, infants might initially have made the prediction that a phone goes to the ear (or that a cup goes to the mouth) based on their prior knowledge, but should have reconsidered this target prediction when the movements started deviating from the path expected from the motor simulation. Additional simulations may account for the finding that the infant's motor system was more strongly activated during the observation of unusual compared to ordinary actions. The movements during the action are thus monitored to reassure that the initial target inference is compatible with the new situation that emerges during the movements. In the study described in Chapter 5, identifying the potential action targets before action onset might have helped the observers to quickly disentangle what would be the action target once the movements started. The idea that the different aspects of an action can play unique roles depending on which phase the action is in deserves more attention in future research. Furthermore, how easily do observers reject the inference they previous held based on prior knowledge and make a new target inference? The predictive coding framework as postulated by Karl Friston (2010) states that inferences are rejected when the prediction error exceeds the criterion set for that particular prediction task. The prediction error is dependent on the generative framework or the world model the observer has. This world model consists of priors, built through experience. The more observations gathered by the observer, the less noisy the prior distribution is. Consequently, the more experienced observer will need less evidence to reject a hypothesis than an observer with a noisier prior. According to this logic, people might become more flexible in target inferences with age and experience. Whether this theoretical assumption is true, requires further empirical testing.

Visuomotor versus motor experience

As outlined in the General Introduction, multiple theories have been proposed on how the action-perception link comes into place during development. The current findings indicate that action prediction abilities differ for different actions and that motor experience with a specific skill ameliorates the prediction quality of exactly that action. The findings are hence congruent with the idea that motor experience plays a key role in the development of the action-perception link, which is consistent with two of the theoretical views discussed in the General Introduction. The first and most widespread view is advocated by Cecilia Heyes and colleagues, who have provided an elegant and clear explanation of how ordinary motor neurons may develop into sensorimotor neurons (also called mirror neurons; Heyes, 2010; Cook et al., 2014). Through the contiguous and contingent experience of acting and receiving sensory information about the consequences of these actions, associations are formed between motor and sensory neurons. Once these associations are formed, perceiving an action will lead not only to the activation of sensory areas of the brain, but also to the activation of the corresponding motor areas. According to Cook and colleagues (2014), this association should be direct: visual information of an action can only evoke a motor response if visuomotor associations have been formed, and similarly, auditory action information can only evoke motor responses if audiomotor associations are present. In this way, own action experience can alter action perception processes.

Alternative to a sensorimotor account including only direct associations with the motor system, a 'motor only' account may also explain action perception development. That is, motor experience may also influence action perception development in the absence of visual experience. It occurs only sporadically that one cannot see the consequences of one's own action. Nevertheless, this does not imply that vision is a necessary component in the development of action perception and action prediction. In an adult study, participants were trained in a novel motor skill while being blind-folded. Their visual recognition of this novel act improved, although they had received a nonvisual motor training (Casile & Giese, 2006). A further challenge for the 'direct sensorimotor' associative learning account are facial movements. Sensorimotor associations for facial expressions are thought to be formed because of being imitated by others (Heyes, 2010). However, such an explanation might seem a bit far-fetched. An infant's smile might trigger her parent to smile back, but other facial expressions, such as crying and the expression of anger and fear, are less likely to be imitated. The role of proprioception in action perception development thus deserves more attention (see also Meltzoff & Moore, 1997). Actors not only receive visual feedback of their action, but also proprioceptive feedback (Scheidt, Conditt, Secco, & Mussa-Ivaldi, 2005). As vision has a higher spatial resolution than proprioception (Driver & Spence, 1998), it would be interesting to investigate whether nonvisual motor training leads to less accurate action prediction than visual motor training.

Both the 'direct sensorimotor' and the 'motor only' account can explain the data of the current set of experiments. Manual actions such as the one presented in Chapter 6 are often guided by vision (Land, 2006; Hayhoe, 2000), whereas actors have only limited visual access to their walking and crawling performance. A third person perspective on walking, crawling, and bringing a cup to the ear is strongly different from the first person perspective. Therefore, the sensorimotor account as presented here needs to be extended in order to fully account for the data presented in Chapters 2, 3 and 5. More specifically, future research on action perception development is needed to clarify how the first person perspective is translated into a third person perspective (Thomas, Press, & Haggard, 2006; Shmuelof & Zohary, 2008) and how this translation is acquired during infancy. A 'motor only' account faces the same challenge of explaining the translation between perspectives. Potentially, proprioception mediates the translation from body-centered into world-centered coordinates and vice versa (Carrozzo, McIntyre, Zago, & Lacquaniti, 1999; Crawford, Medendorp, & Marotta, 2004).

Societal relevance

Beside implications for action perception research, the current research is of relevance for robotics. The demographic transitions resulting from a prolonged life expectancy (Leon, 2011) and decreasing birth rates after the babyboom generation (Lutz, O'Neill & Scherbov, 2004) have caused policy makers in Europe to speculate about using robots to make up for the lack of caretakers for elderly people (Butter et al., 2008; Gelderblom & Rensma, 2010; Bemelmans, Gelderblom, Jonker, & de Witte, 2012). Robots that would be required to smoothly interact with humans will need similar action prediction capabilities as humans have. As mentioned earlier, motor experience may have benefits over and above visual experience when it comes to develop accurate action prediction skills. As motor experience can be gained by the robot without the need of human involvement, motor learning is an interesting mechanism from an economic perspective as well. However, this would imply that robots need to have similar bodily constraints as humans have, which may a drawback regarding the overall functionality of the robot.

Testing theories about the development of human action prediction in robots is advantageous for both research fields, robotics and developmental cognitive neuroscience. Robots (or computational models) offer the most explicit test of mechanisms postulated by (developmental) cognitive neuroscientists (Barsalou, 2008; Harvey et al., 2005; Asada, MacDorman, Ishiguro & Kuniyoshi, 2001), because if the model fails to function in the reality of the robot, the theory can be rejected. Interaction between robotics and developmental cognitive science forces the developmental cognitive scientist to generate testable hypotheses and explicate in detail how they think development works. For instance, the development of gaze following has been captured and described in a computational model which has integrated multiple empirical findings on infants' development of gaze following (Triesch, Jasso, & Deák 2007). Based on the model, new hypotheses about development can be derived. Robotics on the other hand profits from theories about human development, as humans often possess capabilities that roboticists would like to give robots as well. For example, Demiris and Dearden (2005) work on a robot that can learn from others. Their work on the HAMMER model illustrates that motor babbling and motor exploration behavior as found in infants are well-functional mechanisms to provide the robot the capacity to imitate others (Demiris & Dearden, 2005). Development in a robot is sometimes preferable over programming all details in the robot in advance, because it offers flexibility and the potential to adapt to different environments and different situations (Dillmann, 2004). Crossovers between both fields can thus be expected to be fruitful.

Conclusion

The current thesis presents a series of experiments in which action perception and its early development was investigated. Infant and adult observers were shown to base their action predictions on the actor's movements and on their previous knowledge. The developmental findings are consistent with the idea that the capacity to predict others' actions develops through visual and motor experience. Action prediction was found to be more accurate if the observer had motor experience with specifically that action.

Motor or sensorimotor experience can at least have three advantages over observational experience: 1) Prediction of the timing of actions becomes more accurate with motor experience, 2) motor experience allows observers to dissociate which will be the target of an observed action, 3) motor experience serves as a powerful tool to acquire motor laws and information about action constraints that can be used to predict others' actions. The results of the experiments not only provide answers but also make clear that the field is facing several interesting questions. Unresolved is the role of proprioception in active experience with actions: Can nonvisual motor experience explain action prediction development? How can first person experiences be applied to predict actions perceived from a third person perspective relatively quickly after this first person experience has been acquired? Do the separate aspects of actions play a different role during distinct phases of an action? Are there situations in which movements are less important for action prediction than other aspects of the action? More research is needed to further demystify the processes action prediction and its development.

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Nederlandse Samenvatting

Informatiebronnen

Handelingen bevatten verschillende soorten informatie die ofwel onafhankelijk van elkaar danwel in combinatie gebruikt kunnen worden om het toekomstig verloop van een geobserveerde handeling te voorspellen. Mogelijke soorten of bronnen van informatie bestudeerd in dit proefschrift zijn objectkennis, de aanwezigheid van een duidelijk doelwit, de context van de handeling en de bewegingen van de actor. Betreffende objectkennis heeft een eerdere gedragsstudie aangetoond dat de frequentie waarmee de eindlocatie van een handeling voorspeld wordt door baby's en volwassenen, afhangt van het gebruikte object (Hunnius & Bekkering, 2010). Bijvoorbeeld, men verwacht eerder dat een telefoon naar het oor gaat dan een kopje, en men verwacht eerder dat een kopje naar de mond gaat dan een telefoon. Hoofdstuk 2 van dit proefschrift toonde dat de neurale reacties op het bekijken van deze meer of minder voorspelbare object-gerelateerde acties verschillend zijn, wat verdere evidentie is voor de stelling dat objectkennis een rol speelt in actiepredictie.

De resultaten gerapporteerd in de hoofdstukken 2, 4, 5 en 6 illustreren bovendien dat baby's en volwassenen in staat zijn het doelobject of de eindlocatie van een handeling te voorspellen. Objectgerichte handelingen bleken voorspelbaarder te zijn dan niet-objectgerichte handelingen (hoofdstuk 3). Vervolgexperimenten zoals gepresenteerd in hoofdstuk 3, benadrukten echter dat objectgerichte handelingen voorspelbaarder zouden kunnen zijn omdat actoren op een meer voorspelbare manier bewegen als ze naar een doelobject bewegen dan als ze naar niet naar een doelobject bewegen. Deze bevinding gelddde alleen als de handeling beperkt werd door de context, wat suggereert dat de combinatie van het hebben van een ruimtelijk gedefinieerd einddoel én rekening moeten houden met barrières onderweg het aantal vrijheidsgraden van een beweging dusdanig beperkt dat de handeling duidelijk voorspelbaarder wordt.

De rol van kinematica voor actievoorspellingen was diepgravender bestudeerd in de experimenten gepresenteerd in hoofdstuk 5. Daar werd de nauwkeurigheid van de voorspelling van de timing van bewegingen vastgesteld. Kijkers werden geacht hun voorspellingen te baseren op verschillende soorten bewegingen, zoals lopen en kruipen, of de bewegingen van een object. Voorspellingen waren nauwkeuriger voor de menselijke bewegingen dan voor de objectbewegingen. Verder waren de jongste baby's (14-maanden-ouden) accurater in het voorspellen van de timing van kruipen dan van lopen, wat aangeeft dat het soort beweging invloed heeft op actiepredictie.

Het effect van kinematica op actiepredictie was vanuit een andere invalshoek bestudeerd in hoofdstuk 6. Baby's en volwassenen bekeken objectgerichte handelingen die verschilden in snelheid. De resultaten toonden dat de snelheid van een beweging gebruikt wordt in actiepredictie.

Ontwikkelingstijdslijn

De verschillende informatiebronnen die voor actiepredictie worden gebruikt, worden mogelijkerwijs niet allemaal tegelijk geïntegreerd in de actiepredictie van baby's. Het bestuderen van de tijdslijn waarin actiepredictie zich ontwikkelt, zou inzicht kunnen bieden in hoe verschillende competenties op elkaar voortbouwen. Daarnaast zou een ontwikkelingstijdslijn indicaties kunnen verschaffen over de processen die leiden tot de ontwikkeling van actiepredictie, en tegelijkertijd zou een tijdslijn inzicht kunnen geven in de processen die ten grondslag liggen aan actiepredictie in zijn algemeenheid.

Betreffende objectkennis had eerder werk laten zien dat baby's reeds op een leeftijd van 6 maanden doelvoorspellingen kunnen maken op basis van de gebruikte objecten (Hunnius & Bekkering, 2010). Op die leeftijd zijn baby's nog niet in staat alle bestudeerde acties uit te voeren (bijvoorbeeld, het brengen van objecten naar hun oor). Het is daarom uitgesloten dat motorische ervaring ten grondslag ligt aan deze voorspellingen. Daarnaast lijkt het niet waarschijnlijk dat kennis over hoe artefacten normaal gebruikt worden, aangeboren is. Aannemelijker is dat deze voorspellingen verworven worden door visuele ervaringen. Ondanks het feit dat op objectkennis gebaseerde voorspellingen op jonge leeftijd waarschijnlijk worden gemaakt op basis van visuele ervaring, observeerden we in hoofdstuk 2 dat op een leeftijd van 12 maanden, het motorische systeem actief is tijdens objectkennis gebaseerde voorspellingen. Op deze leeftijd zijn baby's in staat de geobserveerde handelingen zelf uit te voeren, want de verzorgers van de deelnemende 12-maanden-ouden rapporteerden dat hun baby dit soort handelingen uitvoerde in het dagelijks leven. Tezamen suggereren deze studies dat hoewel voorspellingen eerst op visuele ervaring gestoeld zouden kunnen zijn, het motorische systeem ook gebruikt kan worden in actiepredictie, zodra de relevante motorische ervaring verworven is.

Voorspellingen van de timing van kruiphandelingen bleken nauwkeurig te zijn vanaf de leeftijd van tenminste 14 maanden; jongere baby's werden in het betreffende onderzoek niet getest (hoofdstuk 5). Baby's worden nauwkeuriger in het voorspellen van de timing van loophandelingen die ze zien tussen een leeftijd van 14 en 20 maanden (hoofdstuk 5). De 20-maanden-ouden hadden meer loopervaring dan de 14-maanden-ouden, aldus hun verzorgers. Voorspellingen van reiken-naar-en-indrukken-van knoppen volgden een ander tijdsbestek qua ontwikkeling: Vijftien-maanden-oude maar niet 12-maanden-oude baby's bleken in staat op basis van de snelheid van de gebruikte hand het doel te voorspellen van een knop-indruk-handeling (hoofdstuk 6).

Processen die ten grondslag liggen aan actiepredictie en de ontwikkeling van actiepredictie

Welke processen liggen ten grondslag aan actiepredictie en de ontwikkeling daarvan? Deze vraag komt terug in bijna ieder hoofdstuk van dit proefschrift. Mijn kernhypothese was dat eigen actie-ervaring de precisie van actiepredictie verbetert. De resultaten suggereren inderdaad dat actie-ervaring een belangrijke rol speelt in de ontwikkeling van actiepredictie. Voorspellingen waren nauwkeuriger voor handelingen die de kijkers in hun motor repertoire hadden dan voor handelingen die ze nog niet in staat waren uit te voeren (hoofdstukken 5 en 6). Het voorspellen van knop-indruk-handelingen bleek te ontwikkelen tussen de 12 en de 15 maanden, wat correspondeert met de tijdslijn van het ontwikkelen van de vaardigheid zelf knoppen in te drukken (hoofdstuk 6). Veertien-maanden-ouden, vaardig in kruipen, bleken een volwassenniveau van nauwkeurigheid te hebben bereikt in het voorspellen van kruipen (hoofdstuk 5). Twintig-maanden-oude peuters, in staat tot zowel kruipen als lopen, toonden even accuraat te zijn in hun voorspellingen van lopen als van kruipen, terwijl 14-maanden-ouden minder accuraat waren in hun voorspellingen van lopen dan van kruipen. Deze bevindingen ondersteunen het idee dat motorische processen cruciaal zijn voor actiepredictie (zie ook hoofdstuk 2), in baby's als ook in volwassenen. Ten slotte stemmen deze bevindingen overeen met het idee dat motorische ervaring fundamenteel is voor de ontwikkeling van actiepredictie.

Curriculum Vitae

Janny Christina Kaars was born in Marken, the Netherlands, on April the 3rd 1983. On April 22^{nd} 2004, Janny married Simeon Stapel and she bears her husband's name since that date. They are the parents of three children. In September 2005, Janny obtained her Bachelor of Science (B.Sc.) degree in Technology and Society from the University of Technology in Eindhoven, the Netherlands, with the distinction cum laude. In the academic year of 2004/2005, Janny was enrolled at Leiden University, the Netherlands, where she took language courses to prepare for a semester abroad. Starting in October 2005, she took part in the Architecture M.Sc. program at Technion in Haifa, Israel, for one semester. In September 2007, she finished the research Master's program in Human Technology Interaction at the University of Technology in Eindhoven (cum laude). She joined the department Human Technology Interaction by researching psychological factors of social interaction over networks, as part of an EU-funded FP6-IST project. In August 2008, Janny started her PhD research at the Donders Institute for Brain, Cognition and Behaviour, the Netherlands, together with her promotor Harold Bekkering and her supervisor Sabine Hunnius. As a member of both the Action and Neurocognition Group and the babyBRAIN group (Baby Research on Action, Interaction and Neurocognition), Janny investigated the role of own action experience in the development of action prediction. During her PhD period, Janny received a Marie Curie Individual Fellowship. This fellowship allows her to continue her research on action prediction development at the Uppsala Child and Baby Lab in Uppsala, Sweden.

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